

# TWO NEW SPECIES AND A REVIEW OF THE SQUID GENUS *ONYCHOTEUTHIS* LICHTENSTEIN, 1818 (OEGOPSIDA: ONYCHOTEUTHIDAE) FROM THE PACIFIC OCEAN

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## ABSTRACT

The onychoteuthid genus *Onychoteuthis* Lichtenstein, 1818 is in systematic disarray. The oldest species, *Onychoteuthis banksii* (Leach, 1817), is widely recognized as a species complex, with which two of the other commonly recognized three species—*Onychoteuthis compacta* (Berry, 1913) and *Onychoteuthis borealijaponica* Okada, 1927—and some 20 additional names have been all synonymized at one time. This study, a partial revision of the genus, redescribes *O. banksii* from the Atlantic Ocean; from the Pacific, *O. compacta*, *O. borealijaponica*, and *Onychoteuthis meridiopacifica* Rancurel and Okutani, 1990, are redescribed, the name *Onychoteuthis aequimanus* Gabb, 1868, is resurrected, and two additional species are described: *Onychoteuthis lacrima* sp. nov., and *Onychoteuthis prolata* sp. nov. Several new species-level characters are examined in detail, compared, and reported for each species, including buccal morphology, tentacular club and hook morphology, chromatophore patterns on the mantle and tentacles, and photophore shape and size.

The cosmopolitan tropical/temperate genus *Onychoteuthis* has long been recognized for its systematic instability (Kubodera et al., 1998; Vecchione et al., 2003). *Onychoteuthis banksii* (Leach, 1817) has been a catch-all name for many morphologically similar taxa since its description nearly 200 yrs ago (Vecchione et al., 2003), including: two of the additional three species generally recognized by recent authors—*Onychoteuthis compacta* (Berry, 1913) and *Onychoteuthis borealijaponica* Okada, 1927, at various times—and about 20 additional nominal species (see e.g., Pfeffer, 1912; Adam, 1952).

In its current state, the name “*O. banksii*” is typically applied to any narrow-bodied *Onychoteuthis* specimen with 20–23 hooks on each tentacular club, two round photophores on the ventral surface of the intestine, ocular photophores, and rhombic fins whose length is ~55% ML, and is widely believed to represent a species complex involving several to many undescribed species (Young, 1972; Nesis, 1987; Young and Harman, 1987; Kubodera et al., 1998; Vecchione et al., 2003).

The confusion surrounding the *Onychoteuthis* taxa stems from a number of separate systematic problems. The type specimens of the four species listed above are, in order, juvenile and damaged (*O. banksii*, Figs. 1, 2); small juvenile and extensively damaged (*O. compacta*, Fig. 3); not extant (*O. borealijaponica*, never designated); and partially digested (*Onychoteuthis meridiopacifica* Rancurel and Okutani, 1990). The original descriptions are, respectively, two lines long and based on a single juvenile specimen; rather more detailed and well-illustrated but based on a single small juvenile; restricted to a description of the visceral photophores only; and relatively more comprehensive but based on partially digested material. Additionally, while *O. borealijaponica* and *O. meridiopacifica* are morphologically distinct, the remaining *Onychoteuthis* species appear similar, and require new characters for reliable differentiation.

Here I examine the Pacific Ocean species of the genus. However, *O. banksii*, originally described from the tropical Atlantic, is also redescribed to differentiate it from the Pacific species. In order to clarify and compare all taxa treated herein—and to provide a basis for comparison of any additional *Onychoteuthis* species recognized from other regions in the future—full morphological redescrptions and illustrations are given for each of the four presently recognized species, one resurrected species (*Onychoteuthis aequimanus* Gabb, 1868, previously described in detail as *O. banksii* from New Zealand waters by Bolstad, 2007), and the two new species.

The present study has resulted from an ongoing systematic revision of the Onychoteuthidae by the author, in addition to the efforts of several colleagues who had independently investigated important characters for diagnosing species within this genus. These colleagues are accordingly named as co-authors on the relevant new species as follows: *Onychoteuthis lacrima* sp. nov. Bolstad and Seki [Seki (2001) first described the paralarva of *O. lacrima* sp. nov. as “species D”]; and *Onychoteuthis prolata* sp. nov. Bolstad, Vecchione, and Young (Vecchione and Young had independently identified several useful characters for separating this species from several other Pacific “forms”).

#### MATERIALS AND METHODS

Original descriptions and, where possible, type material of all previously described nominal *Onychoteuthis* species from the Pacific have been examined.

Preserved and fresh New Zealand onychoteuthid specimens were loaned from, or examined at, the National Institute of Water and Atmospheric Research Ltd (NIWA), and the Museum of New Zealand Te Papa Tongarewa (NMNZ), both in Wellington, and at Auckland University of Technology (AUT), in Auckland, New Zealand. Additional material was loaned from, or examined at, the following institutions: Philadelphia Academy of Natural Sciences, Pennsylvania (ANSP); British Museum of Natural History, London, United Kingdom (BMNH); California Academy of Sciences, San Francisco, California (CASIZ); Zoologisches Museum, Museum für Naturkunde der Humboldt-Universität, Berlin, Germany (MNB); Muséum National d’histoire Naturelle, Paris, France (MNHN); National Marine Fisheries Service, Honolulu, Hawaii (NMFS); Museum of Victoria, Melbourne, Australia (NMV); National Museum of Nature and Science, Tokyo, Japan (NSMT); South African Museum, Cape Town, South Africa (SAM); Santa Barbara Museum of Natural History, California (SBMNH); Rosenstiel School of Marine and Atmospheric Science, University of Miami, Florida (UMML); National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM); and Zoological Museum, Universitetet i Bergen, Norway (ZMBN).

Material collected in the Atlantic on the Dana Expedition (Carlsbergfondets oceanografiske Ekspedition omkring Jorden 1928–1930 under Ledelse af Professor Johannes Schmidt) was examined at (but not part of the collections belonging to) UMML; these specimens are indicated by station numbers beginning with “D,” e.g., D4075 XI.

Some specimens examined in collaboration with R. Young at the University of Hawaii (Honolulu) have not been formally accessioned into a museum collection and have been given temporary reference numbers beginning with KSB (e.g., KSB-001). Type specimens selected from this material and several additional specimens will be accessioned into SBMNH and USNM collections; their temporary KSB-numbers are followed by [SBMNH] or [USNM] to indicate their future location. Collection data for many of these Hawaiian specimens are limited or unavailable; these data have been presented as completely as possible. Incomplete data are followed by “NFD” (no further data). Collection dates are given as dd/mm/yyyy; specimens examined are listed in order of decreasing mantle length (in multiple specimen lots, by ML of the largest specimen). Sexes are provided for the majority of specimens, except in

cases where dissection was unjustified, or where the specimen was too juvenile to determine its sex, indicated "sex indet." Specimens in lots of more than three individuals were generally not sexed.

Distribution maps are based solely on the specimens examined herein; in the Pacific, abundant material was available from the following major currents: North Pacific, North Equatorial, Kuroshio and Kuroshio Extension, California, South Equatorial, and East Australian, and the North and South Equatorial countercurrents. No material was available from the large southeastern gyre formed by the South Pacific, Mentor and Peru currents.

Additional collection acronyms used in text are: CMT, Cobb midwater trawl; EMWT, Engels midwater trawl; FMMWT, fine-meshed midwater trawl; FRV, fisheries research vessel; FTS, fisheries training ship; HN, hand net; IKMWT, Isaacs-Kidd midwater trawl; MBC, Mesopelagic Boundary Community Cruises (conducted by the University of Hawaii); MV, motorized vessel; MWT, midwater trawl; NL, night light; NL&D, night light and dipnet; NN, neuston net; NORFANZ, New Zealand and Australia Norfolk Ridge-Lord Howe Rise Biodiversity Voyage; RFRL, Tokai Regional Fisheries Research Laboratory, Tokyo; RV, research vessel; ST, surface temperature; TC, Townsend Cromwell Cruises (conducted by the University of Hawaii); [x], data lost or illegible (e.g., station number). Morphological acronyms used in text are: ML, mantle length (dorsal), MW (or MWI), mantle width (or mantle width index); HL (or HLI), head length (measured dorsally from anterior tip of dorsal nuchal cartilage to the dorsal separation of Arms I) (or index); HW (or HWI), head width (index); FL (or FLI), fin length (index); FW (or FWI), fin width (index); TnL (or TnLI), tentacle length (index); CL (or CLI), tentacle club length (including carpus) (index); CS, count of carpal suckers; MH, count of manus hooks; MS, count of marginal suckers (on manus); TPS, count of terminal pad suckers; GL, gladius length, with percentages of gladius length (e.g., widest point at 40% GL) measured from anterior extremity of gladius). Measurements of features symmetrical across the midline (e.g., arms, tentacles) were taken on the more complete side of the specimen and are indicated "R" or "L" in the tables. Ranges of indices are given in text as X-Y-Z, where X is the lowest observed value, Y is the mean index, and Z is the highest observed value; in the case of the arms, the range is given as  $X-Y_I-Y_{II-IV}$ -Z, where  $Y_I$  is the mean index of Arms I and  $Y_{II-IV}$  is the mean index of Arms II-IV; where the observed range was less than 5% ML, only the mean is given. The breadths of keels on the arms and tentacle clubs are reported as a percentage of the breadth of the corresponding arm or tentacle at the same point along its length, e.g., an aboral keel that is widest midway along the arm and attains a breadth equal to that of the arm at the same point is described as "attaining 100% arm width at 50% arm length." The swimming keel and lateral membrane breadths on the arms are given as a percentage of the arm dimension visible when the keel is in profile (for Arms I and IV, arm width; for Arms II and III, arm depth).

Specimens photographed using environmental scanning electron microscopy (ESEM) were critical-point dried, coated in gold-palladium, and photographed at the University of Auckland, New Zealand.

Hook terminology follows Young and Harman (1998), with individual hooks identified according to dorsal/ventral row and numbered from proximal-most to distal-most (e.g., first ventral hook, next to carpus = V1; first dorsal = D1); hook length is measured from the proximal lip to the distal extremity of claw (excluding the recurved portion of claw); beak terminology follows Clarke (1980); palatine teeth are observed as in O'Shea (1999) and Bolstad (2007), situated medially on the lateral buccal palps (fide Messenger and Young, 1999). The synonymy for each species is limited to citations providing substantial morphological accounts, including species and specific character descriptions and/or illustrations, and references to type material. Citations not detailed enough to permit confident identification of a taxon, where the material was not available for re-examination, are omitted. Specifically, many references to *O. banksii* in the literature have been excluded, since the characters differentiating species formerly attributed to the *O. banksii* complex have only recently been recognized. Taxa included in genetic studies (e.g., Bonnaud et al., 1998; Wakabayashi et al., 2007) have been

included only where species identity is unambiguous or could be confirmed through re-examination of material.

## SYSTEMATICS

Family Onychoteuthidae Gray, 1847

Genus *Onychoteuthis* Lichtenstein, 1818

*Diagnosis*.—Intestine with two photophores, one over posterior extremity of ink-sac, one near anus; ventral periphery of each eye with one photophore; occipital region with both ventro-lateral (primary) and dorsal (secondary) folds; manus with 15–27 hooks, with bases of ventral hooks asymmetrical, variably produced into spike.

*Onychoteuthis banksii* (Leach, 1817)

(Tables 1, 8, Figs. 1, 2, 4–12)

*Loligo banksii* Leach, 1817: 141.

*Onychoteuthis banksii* (Leach, 1817)—Toll (1982): 51–55, pl. 5A, (1998): fig. 31 — Sweeney and Roper (1998): 572—Lipinski et al. (2000): 106.

*Onychoteuthis banksi* (Leach, 1817)—Clarke (1986): 72–74, fig. 32a.

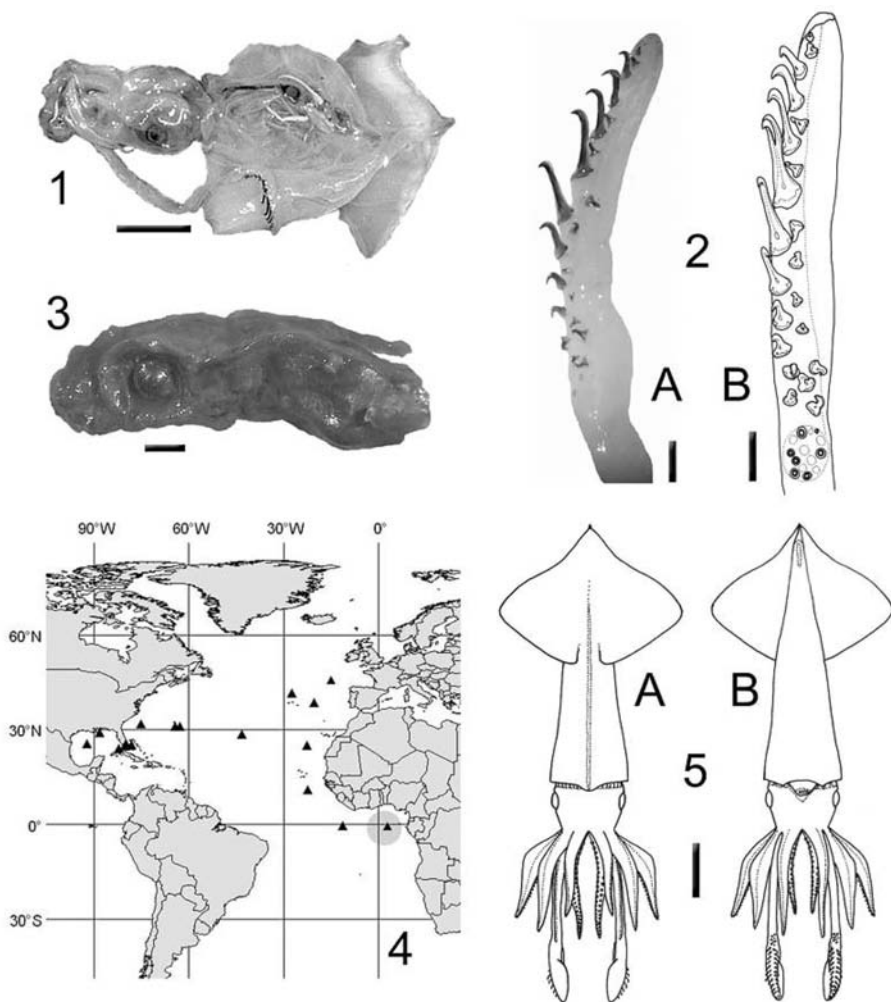
*Distribution* (Fig. 4).—Central and North Atlantic (including Gulf of Mexico); 800–0 m.

*Material Examined* (62 specimens).—BMNH 1986266, holotype, ML 31 mm, Gulf of Guinea, NFD; MNHN 632, ♀, ML 121 mm, coll. d'Orbigny, NFD; MNHN 626, ♀, ML 120 mm, Atlantic Ocean, 1834, coll. d'Orbigny, NFD; UMML 31.2965, ♂, ML 110 mm, 41°37'N, 27°00'W, 500 m, 21/06/1931, 0045 h, Dana 4193 VI; MNHN 633, ♀, ML 91 mm, Atlantic Ocean, 1830, coll. Damon, NFD; USNM 575113 (2 specimens), ♀, ML 88 mm, ♂, ML 77 mm, 28°12'N, 87°49'W, south of Mobile, Alabama, Gulf of Mexico, surface, -/-/1952, RV OREGON Stn 1008, dipnet; UMML 31.984 (24 sex indet.), ML 87–59 mm, 25°21'N, 79°41'W, surface, 27/09/1962, RV GERDA Stn 75; BMNH 20070558, ♂, ML 85 mm, 41°10.5'N, 14°38'W, surface, 28/05/1955, "Discovery" Investigations Stn 3245, HN; CASIZ 030502 (3 specimens), ♂, ML 84 mm, 2 sex indet, ML 76, 62 mm, 25°00'S, 22°20'W, 04/01/1935, Stn N22–23, coll. T. Crocker; CASIZ 030513 (2 specimens), ♂, ML 83 mm, sex indet., ML 67 mm, 33°09'S, 74°12'W, off Chile, 02/02/1935, YACHT ZACA Stn N29, coll. T. Crocker; D4075 XI, ♀, ML 81 mm, 38°29'N, 20°08'E, 600 m, 22/05/1930, 0230 h, Dana Expedition Stn 4075 XI; UMML 31.577 (3 specimens), ♀, ML 73 mm, ♂, ML 70 mm, sex indet., ML 59 mm, 25°20'–24°17.6'N, 78°02'–01.5'W, 1 m over 1071 m, 19/04/1969, plankton net, RV GERDA Stn 1077; UMML 31.1307 (2 ♀), ML 73, 71 mm, 28°28'N, 43°10'W, surface, 18/07/1964, 0330 h, RV GERONIMO Cruise 4, Stn 8, NL&D; UMML 31.39 (2 ♀), ML 70, 66 mm, 23°59'N, 81°48.5'W, between Havana and Key West, -/12/1951, RV YARA (Cuban Navy); D4000, ♀, ML 69 mm, 0°31'S, 11°02'W, surface, 04/03/1930, 0235 h, Dana Expedition Stn 4000; UMML 31.986 (4 sex indet.), ML 68–46 mm, 25°20'N, 79°42'W, surface, 22/06/1962, RV GERDA Stn 40; UMML 31.2058, ♀, ML 63 mm, 25°17'N, 77°55'W, 17/08/1966, RV TURSIOPS Stn 324; USNM 726945, ♀,

Table 1. Measures (mm) and counts of *Onychoteuthis banksii* (Leach, 1817) (arm and tentacle measures recorded from more complete side of specimen, indicated R or L). ML, dorsal mantle length; MW/MWI, mantle width/index (as % ML); HL/HLI, head length/index; HW/HWI, head width/index; FL/FLI, fin length/index; FW/FWI, fin width/index; TnL/TnLI, tentacle length/index; CL/CLI, tentacle club length/index; CS, count of carpal suckers; MH, count of manus hooks, MS, count of marginal suckers; TPS, count of terminal pad suckers.

Specimen ID	BMNH	UMML	UMML	D4075X	UMML	UMML	USNM	USNM	USNM	USNM	USNM	Mean indices
Type Status	1986266	31.2965	None	I	None	31.577	None	726945	885307	727512	575114	575945
ML	31	110	M	F	20	18	73	70	59	53	Indet.	None
Sex	Indet.											
MW	*	21	20	15	18	17	16	16	17	15	11	32
HL	8	20	15	18	17	16	17	17	17	12	11	Indet.
HW	7	15	60	46	55	42	40	34	30	28	29	Indet.
FL	18	77	77	57	23L	29L	22L	19L	20L	16L	16L	10
FW	16	31L	39L	39R	37R	31L	32L	25L	22L	20L	21L	32
Arms I	20L	42L	42L	37R	29L	29L	35L	26L	19L	20L	22L	9L
Arms II	19L	61L	23L	24R	8	7	8	9	7	8R	7	32
Arms III	17L	21	21	21	22	22	22	23	21	21R	22	A1I
Arms IV	43R	0	0	0	0	0	0	0	0	0	0	A2I
TnL	12R	13	13	14	12	15	14	14	13	13R	10	A3I
CL	8	7	7	8	7	8	9	9	7	8R	7	A4I
CS	22	21	21	21	22	22	22	23	21	21R	22	TnLI
MH	*	0	0	0	0	0	0	0	0	0	0	19L
MS	*	13	13	14	12	15	14	14	13	13R	10	9L
TPS	*											27

\* indicates damaged features



Figures 1–5. 1–2: Holotype of *Onychoteuthis banksii*, BMNH 1986266, ML 31 mm. 1: ventral view of whole animal, scale bar = 10 mm. 2: right tentacular club, scale bars = 1 mm. 3: Holotype of *Onychoteuthis compacta*, USNM 214318, ML 21 mm. Scale bar = 10 mm. 4–5: *Onychoteuthis banksii*. 4: distribution of specimens examined; grey circle indicates type locality. 5: USNM 727512, ML 49 mm, (A) dorsal, (B) ventral. Scale bar = 10 mm

ML 59 mm, 31°N, 64°W, Bermuda, 800–0 m, 03/09/1968, RV TRIDENT ACRE 4-1-N; UMML 31.983, ♂, ML 58 mm, 24°35'N, 80°01'W, surface, 13/06/1968, RV GERDA Stn 1006; USNM 885307, sex indet., ML 53 mm, 10°52'N, 22°09'W, 608–592 m, 15/04/1971, 1952–2027h, RV WALTHER HERWIG Stn 490-II-71, 1600-mesh EMWT; USNM 727512, ♀, ML 49 mm, 25°35'N, 79°25'W, Florida, North Atlantic, surface, 22/08/1962, RV GERDA, dipnet and light; USNM 575114, sex indet., ML 48 mm, 25°30'N, 92°00'W, S of Marsh Island, Louisiana, 3162 m [sic], 10/03/1954, RV OREGON, drift net; CASIZ 030487, sex indet., ML 45 mm, 10°01.5'S, 80°05'W, 04/03/1935, Stn N-40; UMML 31.1302, sex indet., ML 45 mm, 31°05'N, 62°35'W, 04/04/1957, MV DELAWARE; UMML 31.701 (2 sex indet.), ML 34, 31 mm, 7°16.2–15.3'N, 79°50.8–52.9'W, 03/05/1967, RV PILLSBURY; USNM 575945 (2 sex indet.), ML 32, 24 mm,



29°00'N, 88°02'W, East of Mississippi River Delta, 247 m, 27/04/1961, RV OREGON 3254, 20 m MWT.

*Diagnosis*.—Intestinal photophores circular, well defined, with diameter of anterior ~75% that of posterior; chromatophores absent from tentacle stalk proximal to carpus; chromatophores present along oro-ventral stalk ridge; tentacle club length ~27% ML, with 20–23 long, slender, strongly recurved hooks; distal-most ventral hook bases not produced into spike.

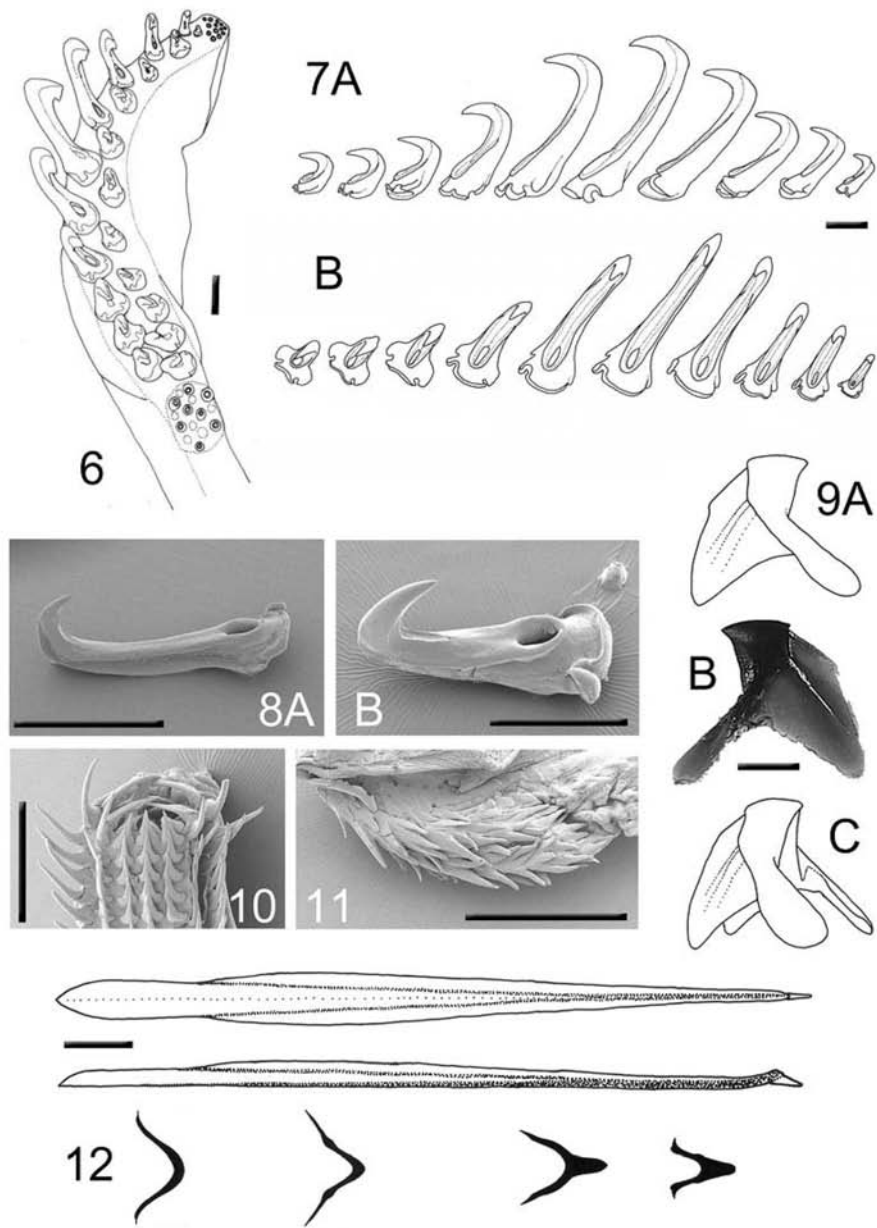
*Description* (Figs. 1, 2, 5–12).—Mantle muscular, width 19–23–27% ML, conical overall, tapering nearly uniformly to slender tail; gladius visible dorsally as prominent ridge along proximal 80% ML; rostrum visible ventrally through distal 10% ML and may pierce tail through at least ML 49 mm; small, firm, oblong ventral keel, ~10% ML, present proximal to visible portion of rostrum. Intestinal photophores circular, with diameter of anterior ~75% that of posterior. Fins rhombic, length ~57% ML, width 52–73–89% ML; posterior margins concave distally, becoming slightly convex proximally; anterior margins straight to slightly convex.

Head rounded, length 18–21–29% ML, width 14–21–29% ML, depth ~19% ML, anteriorly constricted prior to brachial crown; occipital region with six secondary folds. Ocular photophore uniformly broad, with rounded ends, spanning ventral ~30% eye diameter. Funnel groove broad, well-defined V-shape, posteriorly constricted anteriorly into narrow V; funnel aperture opens directly below posterior eye margin. Funnel component of locking apparatus ~15% ML; mantle component ~33% ML.

Arms 28–32<sub>I</sub>–43<sub>II–IV</sub>–48% ML, formula II=III=IV>I, each with 70–80 suckers in two rows, bordered on either side by trabeculate membrane; sucker diameter 40–50% arm width. Aboral keels present on Arms I–III: that on Arms I ~10% arm width over distal 60%–70% arm length; that on Arms II ~50% arm depth over entire arm length; that on Arms III widening to ~100% arm depth by ~30% arm length, thereafter narrowing to arm tip; lateral membrane on Arms IV ~100% arm width along entire arm length.

Tentacles robust, 55–69–80% ML; aboral surface of stalk with low keel, ~15% tentacle thickness, extending from stalk base to level with carpus. Club (Figs. 2, 6) proximally expanded, 21–27–38% ML (42%–54% TnL). Carpus ovoid to oblong, with seven to nine suckers; manus with 20–23 hooks (usually 21 or 22) in two rows (Figs. 2, 7, 8); terminal pad with 10–15 suckers. Hooks D1 and D2 each larger than paired ventral hooks; dorsal hooks thereafter decreasing in size to D4 and D5, which are offset toward midline of club; D6 larger than D5; size of dorsal hooks thereafter decreasing distally. Ventral hooks V1–V6 increase in size distally, with V4 intermediate in size between small proximal hooks and large mid-club hooks; V6 or V7 largest (Fig. 8A), three to four times longer than paired dorsal hook and ~20% club length; distal-most ventral hooks with ventral basal cusp slightly enlarged but not produced into spike (Fig. 8B) (to ML 121 mm). Necks of largest ventral hooks slender, straight in lateral profile; overall recurve of hook in profile 80°–90°. Ventral membrane ~30% club width along entire club length; dorsal membrane ~20% club width, flanking hooks D1–D4 or D5; dorsal keel ~100% club width, flanking dorsal hooks from D3 to club tip.

Lateral profile of lower beak (Fig. 9) longer than deep, with crest sloping steeply downward in nearly straight line, posterior hood edge well above crest, hood length ~50% total crest length, and hood and crest together ~75% baseline; jaw edge straight proximally, becoming slightly concave distally and forming small rostral point; jaw



Figures 6–12. *Onychoteuthis banksii*. 6–8, 10, 11: USNM 727512, ML 49 mm. 9, 12: USNM 575113, ML 88 mm. 6: tentacle club, scale bar = 1 mm. 7: right ventral tentacular hook series, (A) ventral profile, (B) oral view, scale bar = 1 mm. 8: tentacular hooks, (A) right tentacular hook V7, scale bar = 2 mm, (B) right tentacular hook, scale bar = 500  $\mu$ m. 9: lower beak, (A) left, (B) right, (C) left oblique profiles, scale bar = 1 mm. 10: radula, scale bar = 500  $\mu$ m. 11: palatine palp, scale bar = 1 mm. 12: gladius, scale bar = 10 mm



angle obtuse, slightly obscured laterally by low, rounded, indistinct wing fold. Shoulder ridge distinct, sharp; angle ridge well developed, spanning ~80% lateral wall depth; angle point distinct, darkly pigmented; wings broaden distally, width ~130% that at jaw angle, length ~170% LRL, with small triangular insert of cartilage below jaw angle; crest broad, not thickened; lateral wall diagonally bisected by dark, prominent shelf anteriorly, becoming low, rounded ridge posteriorly, curving slightly and becoming indistinct by ~75% distance between rostral tip and posterior lateral wall corner.

Radula (Fig. 10) with unicuspid rachidian, with broad triangular mesocone and low, broad, rounded base, its height ~25% that of entire rachidian height. First lateral tooth unicuspid, slightly shorter and more narrow than rachidian, straight or slightly curved, slightly medially directed, with base shorter on inner edge of tooth than outer (sometimes indistinguishable on inner edge). Second lateral tooth simple, slender, slightly curved, ~150% height of rachidian. Marginal tooth simple, slightly curved or straight proximally, curving only at tip, ~200% height of rachidian. Palatine palp (Fig. 11) with ~70 long, robust teeth, each 70%–230% rachidian height, densely distributed over palp.

Gladius (Fig. 12) with greatest width (~7% GL) attained at ~45% GL; free rachis ~20% GL; vanes broaden rapidly between 20 and 50% GL, gradually narrowing thereafter; dorsal keel solid, deep, comprising ~50% gladius depth at ~80% GL. Rostrum ~5% GL, triangular in lateral profile, narrow in dorsal profile.

*Remarks.*—The holotype of *O. banksii*, from the Gulf of Guinea, is juvenile (ML 31 mm), and its tissues appear somewhat stretched (Fig. 1). The intestinal photophores on this specimen are, however, intact and the ventral hooks on the remaining (right) tentacle club (Fig. 2) are long and slender. These characters and their states are of considerable systematic value, and are shared with Atlantic specimens herein attributed to *O. banksii*, one of which was collected near the type locality. This species is not currently known from the Pacific Ocean. It occurs commonly at the surface at night, with the majority of specimens quite remarkably having been found on ship decks.

### *Onychoteuthis aequimanus* Gabb, 1868

(Tables 2, 8, Figs. 13–19)

*Onychoteuthis aequimanus* Gabb, 1868: 23, 24, pl. 2—Spamer and Bogan (1992): 1. *Onychoteuthis banksi* (not Leach, 1817)—Dell (1951): 99—Imber and Russ (1975): 30—Imber (1976): 124.

*Onychoteuthis banksii* (not Leach, 1817)—Dell (1951): 102, fig. 6, (1952): 100, 101, tables 27, 28, Pl. 20.

? *Onychoteuthis* sp. C Young and Harman, 1987: 313–321, figs. 1–4, 6, 8—Sweeney et al. (1992): 129, fig. 181—Seki (2001): 44–50.

*Onychoteuthis "banksii"* (not Leach, 1817)—Bolstad (2007): 308–314, tables 1, 6, figs. 2–13.

*Distribution* (Fig. 13).—Pacific Ocean, south of 30°N; known from Hawaiian and New Zealand waters, Palmyra Island, and the Society Islands.

*Material Examined* (65 specimens).—ANSP 6444 (2 ♂), syntypes, ML 93 mm, 80 mm, Society Islands, NFD; NMNZ M.74145 (2 ♀), ML 138, 137 mm, 240 km SW of

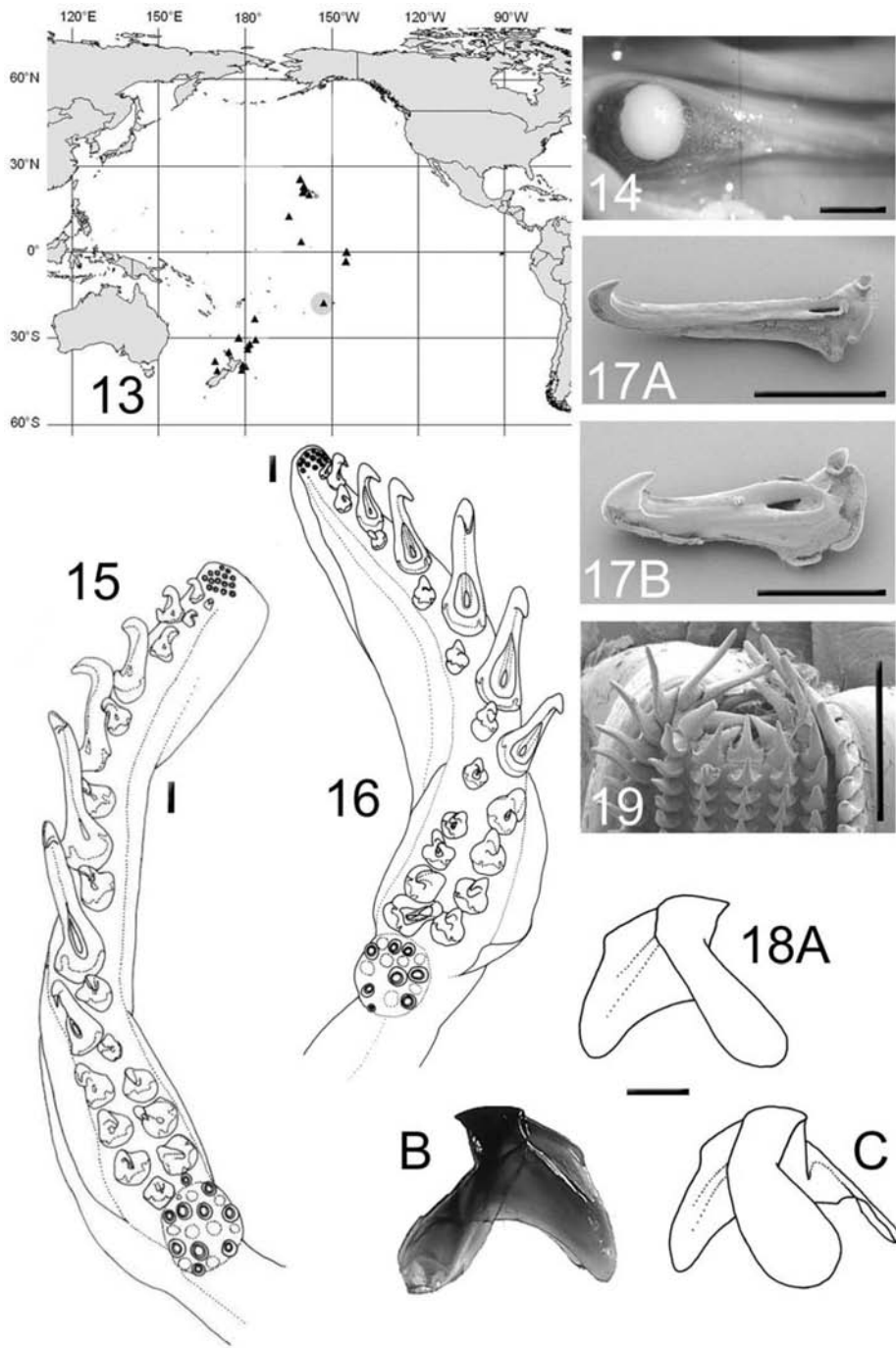
Table 2. Measures (mm) and counts of *Onychoteuthis aequimanus* Gabb, 1868 (arm and tentacle measures recorded from more complete side of specimen, indicated R or L). See Table 1 for abbreviations.

Specimen ID	ANSP	ANSP	NMNZ	USNM	KSB-028	USNM	KSB-024	KSB-005	USNM	KSB-026	NMNZ	Mean indices
Type Status	6444	6444	M.74145	813414	None	813414	None	None	813433	None	M.91480	
ML	Syntype	Syntype	None	None	None	None	None	None	None	None	None	
	93	80	137	100	108	100	99	70	65	44	25	(ML 65–137)
Sex	M	M	F	M	F	M	M	F	F	M	Indet.	
MW	19	17	35*	28	25	28	26	18	12	12	7	MWI
HL	18	19	33*	24	22	24	16	22	17	10	12	HLI
HW	18	15	37*	15	15	15	11*	17	15	9	16	HWI
FL	49	48	75	53	60	53	54	38	38	24	5	FLI
FW	56*	50	105	78	74	78	72	51	52	32	6	FWI
Arms I	37R	27R	57L	36L	32L	36L	33L	22L	26R	12R*	6L	AII
Arms II	49R	32R	77L	48L	46L	48L	46L	20L	33R	17R	8L	A2I
Arms III	50R	32R	81L	46L	47L	46L	45L	31L	32R	17R	8L	A3I
Arms IV	39R	31R	74L	56L	54L	56L	51L	34L	34R	18R	8L	A4I
TnL	95R	60R	160L	94L	118L	94L	126L	73L	51R	41R	13L	TnLI
CL	24R	17R	41L	30L	34L	30L	30L	21L	21R	14R	6L	CLI
CS	6	8	7L	7	7	7	8	7	9	7	6	
MH	23	23	22	19	21	19	20	21	21	21	V3–11, D just forming	
MS	0	0	0	0	0	0	0	0	0	0	all	
TPS	*	*	14	12	13	12	14	15	13	12	11	

\* indicates damaged features

Esperance Rock, Kermadec Islands [ $\sim 33^{\circ}\text{S}$ ,  $179^{\circ}\text{E}$ ], 01/04/1973, RV *ACHERON*, flew/washed aboard; NMNZ M.74508 (4 specimens), ♀, ML 122 mm, 3 sex indet., ML 110–61 mm, FRV *JAMES COOK* Stn J01/[x]/76, NFD; NMNZ M.91739, ♂, ML 110 mm, S. of Kermadec Islands [ $\sim 29^{\circ}17'\text{S}$ ,  $177^{\circ}55'\text{W}$ ], coll. R. Grace, NFD; KSB-023 (2 ♀), ML 108, 106 mm,  $20^{\circ}59.4'\text{N}$ ,  $159^{\circ}42.6'\text{W}$ , 28–29/01/1982, FTS *HOKUSEI MARU* 82-02 Stn 12 (HOG 8201), surface gillnet, coll. M. Seki, NMFS Ref Ceph-0006; KSB-028 (2 ♀), ML 108, 58 mm, 1–0 m over  $\sim 500$  m, 31/10/1989, 0410–0500 h, TSUJI IV, Tow 48B, NN, NFD; NMNZ M.160477 (3 specimens), ♂, ML 106 mm, ♀, ML 90 mm, sex indet., ML 79 mm,  $37^{\circ}\text{S}$ ,  $167^{\circ}\text{E}$ , winter 1960, coll. N.W. Thomas, “flew” on board; NMNZ M.91593, ♂, ML 100 mm,  $39^{\circ}09.7'\text{S}$ ,  $179^{\circ}38.8'\text{E}$ , 35 m, 31/05/1987, FRV *JAMES COOK*; USNM 813414 (2 ♂), ML 100, 96 mm, Oahu, Hawaii [ $21.5^{\circ}\text{N}$ ,  $158^{\circ}\text{W}$ ], surface, 29/04/1957, RV *HUGH M. SMITH* Stn 39-[x], NL&D; KSB-024, ♂, ML 99 mm,  $21^{\circ}39.2'\text{N}$ ,  $158^{\circ}59.0'\text{W}$ , 30–31/01/1982, coll. M. Seki, FTS *HOKUSEI MARU* 82-01 Stn 23 (HOG 8203), surface gill net, 30 mm mesh, NMFS Ceph-0008; KSB-022, ♂, ML 97 mm,  $21^{\circ}00.5'\text{N}$ ,  $158^{\circ}51'\text{W}$ , 31/01/1982–01/02/1982, surface gillnet, FTS *HOKUSEI MARU* 82-01 Stn 29 (HOG 8204), coll. M. Seki, NMFS Ref Ceph-0011; NMNZ M.74494 (2 ♀), ML 94, 81 mm,  $31^{\circ}04'\text{S}$ ,  $175^{\circ}04'\text{W}$ , 70 m over 5000+m, 04/12/1976, FRV *JAMES COOK*; NIWA 32735, ♂, ML 92 mm,  $40^{\circ}51'\text{S}$ ,  $178^{\circ}20'\text{E}$ , 100–20 m over 3064 m, -/02/2002, RV *TANGAROA* Stn TAN9802/172, FMMWT; NMNZ M.91594, ♀, ML 84 mm,  $38^{\circ}58.8\text{--}57.6'\text{S}$ ,  $178^{\circ}38.7\text{--}40'\text{E}$ , 35 m, 01/06/1987, FRV *JAMES COOK* Stn J7/10/87, FMMWT; NMNZ M.160464, ♀, ML 79 mm,  $41^{\circ}13.8'\text{S}$ ,  $176^{\circ}51.6'\text{E}$ , 800 m over 1378–996 m, 31/07/1985, FRV *JAMES COOK* Stn J10/01/85; NMNZ M.160454, sex indet., ML 76 mm,  $41^{\circ}41.2'\text{S}$ ,  $168^{\circ}44.2'\text{E}$ , 1056–1043 m, 16/10/1983, FV *ARROW* Stn A02/132/83; KSB-005 [SBMNH], ♀, ML 70 mm,  $21^{\circ}43'\text{N}$ ,  $157^{\circ}51'\text{W}$ , off northeast Oahu, 1–0 m over 472 m, 22/09/1992, 2247 h, ST  $26.5^{\circ}\text{C}$ , RV *WECOMA*, Tsuji Cruise, NN; NMNZ M.74491, sex indet., ML 66 mm,  $33^{\circ}14'\text{S}$ ,  $179^{\circ}14'\text{W}$ , 695 m over 3000+m, 04/12/1976, FRV *JAMES COOK*; USNM 813433, ♀, ML 65 mm, Kaoko, Hawaiian Islands,  $19^{\circ}21'\text{N}$ ,  $162^{\circ}05'\text{W}$ , surface, 23/07/1951, RV *J.R. MANNING* 7-B-1, NL&D; KSB-004, ♀, ML 62 mm, 1–0 m over 500 m, 07/01/1992, 2213 h, NN, MBC Cruise 3, Tow 3018, NFD; NMNZ M.74537 (2 sex indet.), ML 62, 46 mm,  $35^{\circ}06'\text{S}$ ,  $179^{\circ}20'\text{W}$ , 774 m over 3000+m, 03/12/1976, FRV *JAMES COOK*; KSB-057, ♀, ML 54 mm,  $25^{\circ}28.2'\text{N}$ ,  $160^{\circ}42.0'\text{W}$ , 28/03/1992, 2113–2213 h, CMT, TC 92-02 Stn 40, NMFS S-0408; KSB-027, sex indet., ML 52 mm, 1–0 m over 800 m, 26/10/1989, 2003 h, TSUJI IV, Tow 19B, NN, NFD; KSB-031, ♂, ML 50 mm, off Oahu, 800–0 m, 1200–2000 h, FTS *HOKUSEI MARU* Trawl #1, Stn 1; NMNZ M.74553, sex indet., ML 43 mm,  $23^{\circ}08'\text{S}$ ,  $175^{\circ}30'\text{W}$ , 348 m over 1000+m, 08/12/1976, 1833–1933 h, FRV *JAMES COOK* Stn J017/047/76; KSB-025, sex indet., ML 43 mm, north coast of Palmyra Island [ $\sim 5^{\circ}53'\text{N}$ ,  $162^{\circ}05'\text{W}$ ], 1–0 m over  $\sim 500$  m, 16/12/1989, 2156–2258 h, NN, L/A-N9; KSB-026 [SBMNH] (2 specimens), ♂, ML 44, sex indet., ML 35 mm,  $22^{\circ}50.4'\text{N}$ ,  $159^{\circ}35.1'\text{W}$ , 26/03/1992, 1955–2055 h, TC 92-02, CMT, NMFS S-0309; NMNZ M.91480 (25 sex indet.), ML 37–13 mm,  $34^{\circ}20.6\text{--}19.5'\text{S}$ ,  $173^{\circ}29.7\text{--}27.7'\text{E}$ , 150 m over 1558–1453 m, 25–26/10/1985, FRV *JAMES COOK* Stn J16/32/85, FMMWT.

*Diagnosis.*—Intestinal photophores circular, well defined, with diameter of anterior  $\sim 40\%$ – $60\%$  that of posterior; chromatophores forming reduced band across dorsal half to one-third tentacle stalk width orally, proximal to carpus; chromatophores absent from oro-ventral tentacle stalk ridge, and from small patch on ventral surface of mantle (distal  $\sim 15\%$  ML); tentacle club length  $\sim 28\%$  ML, with 19–23 long, slen-



Figures 13–19. *Onychoteuthis aequimanus*. 13: distribution of specimens examined; grey circle indicates type locality. 14: posterior visceral photophore, KSB-057, ML 54 mm, scale bar = 2 mm. 15: right tentacular club, syntype, ANSP 6444, ML 93 mm, scale bar = 1 mm. 16: left tentacular club, KSB-005, ML 70 mm, scale bar = 1 mm. 17: tentacular hooks, KSB-031, ML 50 mm, (A) left tentacular hook V7, scale bar = 2 mm, (B) left tentacular hook V10, scale bar 500  $\mu$ m. 18: lower beak, KSB-022, ML 97 mm, (A) left, (B) right, (C) left oblique profiles, scale bar = 1 mm. 19: radula, KSB-022, ML 97 mm, scale bar = 500  $\mu$ m

der hooks, shallowly recurved ( $90^{\circ}$ – $100^{\circ}$ ) in lateral profile; distal-most ventral hook bases may develop into low spike above ML 90 mm.

*Description* (Figs. 14–19).—Mantle muscular, conical, width 17–24–31% ML; gladius visible along proximal  $\sim 85\%$  of dorsal midline as dark, raised ridge; rostrum of gladius visible ventrally through distal  $\sim 5\%$  ML; distal portion of rostrum may pierce tail in specimens to ML  $\sim 70$  mm; low, narrow medial keel present along distal 20% of ventral mantle surface. Fins rhombic in outline, length  $\sim 55\%$  ML, width 64–72–86% ML at ML  $> 70$  mm,  $\sim 80\%$  ML at ML  $< 70$  mm, slightly narrowed and extended posteriorly; posterior margin concave over posterior third, thereafter straight to slightly convex; anterior margin straight to slightly convex; anterior lobes broad, shallow. Intestinal photophores well defined, circular in outline; diameter of anterior  $\sim 40\%$ – $60\%$  that of posterior; ink sac often swollen beneath posterior photophore, creating distinctive “bulging” appearance (Fig. 14).

Head boxy, length 16–24–31% ML; width 14–18–24% ML; occipital region with seven to ten secondary folds. Ocular photophore broad, rounded at both ends, of uniform breadth along its length, spanning ventral  $\sim 30\%$  eye circumference. Funnel groove deep, broadly V-shaped posteriorly, with acute anterior angle, bordered by low, fleshy ridge; funnel component of locking apparatus  $\sim 15\%$  ML; mantle component  $\sim 26\%$  ML.

Arms 30–35<sub>I</sub>–46<sub>II–IV</sub>–59% ML, formula II=III=IV>I (or IV>II=III>I, mostly in specimens of ML 70–110 mm); each arm with 90–110 suckers by ML 70 mm. Keels present on Arms I–III: that on Arms I  $\sim 25\%$  arm width over distal 50% arm length; that on Arms II  $\sim 50\%$  arm depth over proximal 25% arm length, thereafter  $\sim 75\%$  arm depth to tip of arm; that on Arms III attaining  $\sim 150\%$  arm depth in medial 30% arm length, thereafter narrowing to arm tip; lateral membrane on Arms IV  $\sim 100\%$  arm width over proximal 25% arm length, narrowing thereafter to  $\sim 75\%$  arm width along remainder of arm length.

Tentacles 75–104–127% ML, with low aboral keel ( $\sim 10\%$  stalk thickness) along stalk. Clubs 21–28–31% ML (25%–40% TnL) (Figs. 15, 16), with six to nine carpal suckers, 19–23 manus hooks (Figs. 17A,B) and 11–15 terminal pad suckers. Proximal ventral hooks variably sized, subequal to, larger or smaller than paired dorsal hooks; largest ventral hook (V6 or V7, Fig. 17A) five to seven times larger than paired dorsal hook and  $\sim 20\%$  CL; longest ventral hooks slender, slightly curved in lateral profile; claw weakly recurved at  $\sim 90^{\circ}$ – $100^{\circ}$ . Bases of distal-most ventral hooks asymmetrical, but not produced ventrally into spike in individuals of ML  $< 90$  mm (Fig. 17B); small spike may develop at larger MLs. Hooks D4 and D5 smaller than D1–D3 and offset toward centre of club. Ventral membrane  $\sim 75\%$  club width along entire club; dorsal membrane  $\sim 5\%$  club width, flanking hooks D1–D4; dorsal keel originates near hook D3 and attains  $\sim 125\%$  club width near hook D8.

Lateral profile of lower beak (Fig. 18) longer than deep, with crest sloping steeply downward in nearly straight line, posterior edge of hood close to crest, hood length  $\sim 40\%$  total crest length, and hood and crest together  $\sim 80\%$  baseline; jaw edge slightly concave; jaw angle obtuse, slightly obscured laterally by low, rounded, indistinct wing fold. Shoulder ridge distinct, sharp; angle ridge spans 40%–60% lateral wall depth; angle point darkly pigmented, not raised; distal wing width  $\sim 140\%$  that at jaw angle, wing length 170%–200% LRL, with small semicircular insert of cartilage below jaw angle; crest broad, not thickened or only slightly thickened; lateral wall



not indented below crest, diagonally bisected by dark, prominent ridge, remaining distinct to lateral wall corner.

Radula (Fig. 19) with tricuspid rachidian, with narrow triangular mesocone and narrow, rounded lateral cusps, their height ~25% that of mesocone height. First lateral tooth unicuspid to slightly bicuspid; inner cusp straight, slightly shorter than rachidian and of similar breadth, slightly medially directed; outer cusp (where present) low (~25% height of inner cusp), pointed, slightly laterally directed. Second lateral tooth simple, robust, straight, short, ~120% height of rachidian. Marginal tooth simple, straight proximally, curving distally to slightly laterally directed tip, ~200% height of rachidian. Palatine palp with ~35 robust, flat teeth, each 130%–200% rachidian height, sparsely set in approximately transverse rows.

Gladius with greatest width (~8% GL) attained at ~45% GL; free rachis ~20% GL; vanes broaden and taper rapidly between 20% and 60% GL; dorsal keel solid, narrow. Rostrum ~5% GL, triangular in lateral profile, narrow in dorsal profile.

Color (preserved) deep purple-red, darkest dorsally on mantle and fins, surrounding very dark red-brown keel of gladius; small distal portion of ventral mantle surface (~15% ML) unpigmented; head dark dorsally, paling laterally and ventrally apart from pronounced darkening on dorsal lobe of anterior eye sinus; chromatophores present over all external funnel surfaces and within groove; arms darkest on aboral surfaces, with few oral chromatophores; tentacle stalks dark aborally, pale orally; chromatophores absent from ventral stalk ridge and present only in small dorsal cluster proximal to carpus.

*Remarks.*—*O. aequimanus* was described from two specimens taken near the Society Islands (Gabb, 1868), but was subsequently synonymized with *O. banksii* by Adam (1952) and Voss (1962). However, Young and Harman (1987) recognized the presence of at least three *Onychoteuthis* species in Hawaiian waters, and Seki (2001) also concluded that each was distinct, in addition to *O. borealijaponica* and a fourth species, *O. lacrima* sp. nov. (his “sp. D”).

Gabb (1868) noted that the *O. aequimanus* syntypes had been preserved in alcohol for a significant amount of time before he received them, and consequently had lost much pigmentation. The soft tissues of the syntypes have also hardened, the tentacles appear stretched, and the hooks somewhat desiccated. Nevertheless, apart from chromatophore patterns, the important characters (photophores, club morphology (Fig. 15), overall body proportions, beak and radula) are in sufficient condition to permit comparison with material reported herein. Strong similarities in morphology are observed between the *O. aequimanus* types, similar-sized specimens from Hawaii provisionally attributed to Young and Harman’s (1987) “species C,” and *O. banksii* (sensu Bolstad, 2007) specimens from New Zealand; the differences between these specimens and other Pacific species are also consistent. Therefore, *O. banksii* (sensu Bolstad, 2007) from New Zealand, and provisionally “species C” (Young and Harman, 1987) are attributed to the existing name *O. aequimanus* Gabb, 1868.

The ink sac “bulge” (see Fig. 14) observed in the *O. aequimanus* syntypes and in other material attributed to this species may be a preservation artifact, although it has not been reported or observed in any other taxon.

*Onychoteuthis compacta* (Berry, 1913)

(Tables 3, 8, Figs. 3, 20–27, 59A)

*Teleoteuthis compacta* Berry, 1913: 565—Berry (1914): 324, fig. 32—Roper and Sweeney (1978): 5.

*Onychoteuthis compacta* (Berry, 1913)—Young and Harman (1987): 313–321, figs. 1–6, tables 1–3—Sweeney et al. (1992): 129, fig. 179—Bizikov (1996): figs. 3, 4—Kubodera et al. (1998): 279, fig. 5—Sweeney and Roper (1998): 571—Seki (2001): 44–50—Okutani (2005): 154—Wakabayashi et al. (2007) 959–965, table 2, fig. 2.

*Onychoteuthis banksi* (not Leach, 1817) — Hess (1987): 288, 289, 300, 301, fig. 54a–c.

*Pacific Distribution* (Fig. 20).—Central Pacific, primarily 30°N–30°S. Depth distribution unknown; majority of specimens collected at surface. Also known from western North-Central Atlantic, primarily 0°–40°N (Bolstad, unpubl. data).

*Material Examined* (47 specimens).—USNM 214318, holotype, sex indet., ML 21 mm, 22°00'N, 159°30'W, off Kauai Island, Hawaii, 915–704 m, 11/06/1902, ALBATROSS 3989; KSB-055, ♀, ML 130 mm, Holoikua, Pearl and Hermes Atoll [~27°50'N, 175°50'W], on deck, 08/04/1980, TC 80-02; KSB-060, ♀, ML 125 mm, Pearl and Hermes Atoll [~27°50'N, 175°50'W], on deck, 08/04/1980, TC 80-02; KSB-021, ♂, ML 127 mm, ~30°N, 178°W, on deck, 3–4/08/1991, 1900–0600 h, TC 91-06, NMFS S-0272; KSB-006, ♂, ML 123 mm, 18°54'N, 157°50'W, on deck, 02/05/2001, 0700 h, TC 01-04; KSB-059, ♂, ML 119 mm, Pearl and Hermes Atoll [~27°50'N, 175°50'W], on deck, 09/04/1980, TC 80-02; KSB-013, ♀, ML 118 mm, 24°36'N, 170°53.6'W, 93 km NW of Maro, 03/07/1990, TC 90-05 Stn 125; USNM 813415, ♀, 114 mm, 01°52'N, 157°20'W, off Christmas Island, Line Islands, 20/02/1967, RV C.H. GILBERT 98-[x], NL&D; USNM 813416, ♂, ML 112 mm, 21°24'N, 157°44'W, off Kailua, 07/08/1970, RV H.M. SMITH Stn 3-[x], NL&D; USNM 813422 (3 specimens), ♀, ML 112 mm, 2 ♂, ML 108, 85 mm, 28°13'N, 177°22'W, Fishing dock, Midway Island, 50–0 m, 29/05/1956, RV J.R. MANNING Stn 31-2, NL&D; KSB-017, ♂, ML 106 mm, 27°15'N, 158°W, on deck, 27/04/1998, TC 98-05 Stn 26; KSB-012, ♀, ML 98 mm, 6 km north of Laysan Island [~25°46'N, 171°44'W], on deck, 06/06/1980, TC 80-03; NSMT Mo66881, ♀, ML 97 mm, 34°04'N, 140°06'E, 24/07/1971, surface, 0900 h, RV SOYO-MARU Stn B2, coll. N. Sato, HN; NSMT Mo66888 (2 ♀), ML 97, 84 mm, 29°00'N, 135°00'E, -/06/1969, NFD; USNM 813400, ♀, ML 96 mm, 05°N, 130°W, Line Islands, 12/11/1952, RV H.M. SMITH Stn 18-33, CMT; USNM 813394, ♀, ML 93 mm, 29°59'N, 164°49'W, Hawaii, 25/08/1955, RV H.M. SMITH, 3 m IKMWT; USNM 813410 (4 specimens), ♂, ML 92 mm, 3 sex indet., ML 59–52 mm, 20°52'S, 173°31'W, 10/03/1962, CMT, RV C.H. GILBERT Stn 55-93; NSMT Mo66885, ♂, ML 91 mm, 24°10'N, 154°35'E, 17/04/1970, NFD; UMML 31.2343, ♂, ML 90 mm, 10°29'N, 113°58.6'W, 03/02/1964, RV SOYO-MARU Cruise 13 Stn 247, coll. W. Klawe, NL; USNM 813428 (2 specimens), ♀, ML 89 mm, ♂, ML 63 mm, 20°09.5'N, 171°30'W, Hawaiian Islands [label says 71°], surface, NL&D, 13/10/1963, RV SILVER BAY; USNM 813413, ♀, ML 88 mm, 36°11'N, 149°00'W, 22/07/1955, RV J.R. MANNING Stn 26-7, NL&D; KSB-014 (2 ♀), ML 88, 88 mm, 27°45.04'N, 167°30.02'W, on deck, 13/05/1997, 0607–0637 h, TC 97-04 Stn 138, CTD cast 079, coll. BCM, JFP; KSB-016, ♀, ML 88 mm, 27°15'N, 158°W, 27/04/1998, TC 98-05 Stn 26, flew on deck; USNM 813423 (2 ♀), ML 85, 47 mm, 00°28'N, 169°54'W, Line Islands, surface, 24/06/1951, coll. NMFS, NL&D; USNM 813411, ♀, ML 76 mm, 17°46'S, 176°12'E, 21/02/1962, CMT, RV C.H. GILBERT Stn 55-58; USNM 813395 (2



specimens) ♀, ML 75 mm, sex indet., ML 61 mm, 34°23'N, 150°07'W, 21/07/1955, RV J.R. MANNING Stn 26-5, CMT; USNM 813424, ♀, ML 75 mm, 18°35'N, 159°18'W, Hawaii, 30/06/1951, coll. NMFS-HI, NL&D; USNM 813385, ♀, ML 73 mm, 10°N, 158°W, 1006-0 m, -/02/1950, RV H.M. SMITH Stn 2-36, CMT; BMNH 20070479, ♀, ML 71 mm, 31°N, 125-129°W, 30/01/1981, pres. P. Horsman; USNM 727512, ♀, ML 67 mm, NFD; KSB-015, sex indet., ML 67 mm, 27°15'N, 172°W, on deck, 01/05/1997, 1000 h, coll. J. Palmer, TC 97-04 Stn 8; USNM 813434 (2 sex indet.), ML 61, 49 mm, 03°11'N, 168°07'W, 25/06/1951, NL&D, NFD; KSB-020 [SBMNH], ♀, ML 59 mm, 15°N, 159°16.8'W, surface, 24/04/2001, TC 01-04 Stn 15 Sample 1; USNM 813365, ♀, ML 54 mm, 18°22'N, 147°09'W, 20-0 m, -/03/1959, CMT; USNM 813390, ♂, ML 54 mm, 15°03'S, 170°47'W, 13/03/1962, RV C.H. GILBERT Stn 55-103, CMT; USNM 812435, ♀, ML 47 mm, 02°01'S, 171°37'W, 23/06/1951, NL&D, NFD.

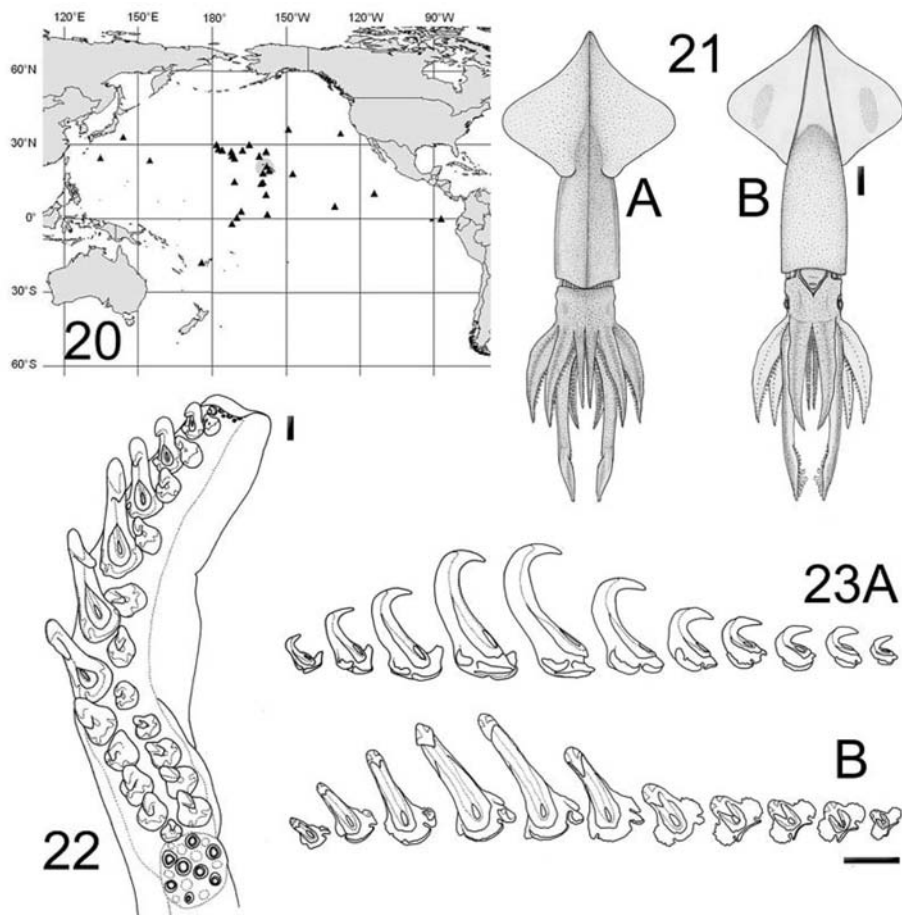
*Diagnosis.*—Intestinal photophores circular, well defined, with diameter of anterior 30%–50% that of posterior; chromatophores absent from tentacle stalk proximal to carpus from oro-ventral stalk ridge, and from large patch on ventral surface of mantle (distal ~40% ML); tentacle club length 17%–23% ML, with 20–23 short, robust, strongly recurved (70°–90°) hooks, with curved necks in lateral profile; distal-most ventral hook bases with large spike.

*Description* (Figs. 21–27).—Mantle conical overall, widening slightly midway along ML, width 20–26–30% ML at ML < 100 mm, 20%–24% ML at ML > 100 mm; gladius visible dorsally as prominent ridge along proximal 90% ML; rostrum visible ventrally through distal ~7% ML and may pierce tail in individuals to ML 63 mm. Intestinal photophores circular, with diameter of anterior 30%–50% that of posterior. Tail slender, with small, firm, oblong ventral keel, its length ~10% ML. Fins rhombic, length ~56% ML; width 57–77–90% ML; anterior and posterior margins straight, becoming slightly concave distally along tail.

Head rounded, length 16–20–25% ML, width 16–20–25% ML, depth ~17% ML, constricted anteriorly; occipital region with seven or eight secondary folds; funnel groove broad, well-defined V-shape; funnel aperture level with midpoint of eye. Ocular photophore somewhat broader posteriorly than anteriorly, rounded at both ends, spanning ventral ~40% eye circumference. Funnel component of locking apparatus 13%–15% ML; mantle component 25%–33% ML.

Arms 30–32<sub>I</sub>–42<sub>II–IV</sub>–51% ML, formula II=III=IV>I, each with 70–100 suckers at ML ~100 mm, 90–110 suckers at ML > 100 mm; oral faces of arms bordered on either side by trabeculate membrane; sucker diameter ~40%–50% arm width. Aboral keels present on Arms I–III: that on Arms I ~10% arm width over distal 60%–70% arm length; that on Arms II ~30% arm depth over proximal 30% arm length, thereafter ~100% arm depth; that on Arms III ~25% arm depth over proximal 25% arm length, thereafter ~100% arm depth; lateral membrane on Arms IV ~100% arm width proximally, narrowing to 75% arm depth by 25% arm length.

Tentacles robust, 48–61–97% ML; aboral surface of stalk with low keel (~15% tentacle thickness) extending from stalk base to level with carpus. Club (Figs. 22, 59A) slightly expanded, 20–22–23% ML (32%–40% TnL); carpus compact, nearly circular in outline, with six to ten suckers (usually eight or nine); manus with 20–23 hooks (usually 21 or 22) (Figs. 23, 24); terminal pad with 12–14 suckers. Proximal ventral hooks variably sized (smaller than, equal to or slightly larger than paired dorsal hooks); hooks V1–V4 or V1–V5 small, subequal in size; V5 transitional between small proximal and large mid-club ventral hooks; V6 and V7 (Fig. 24A) largest on

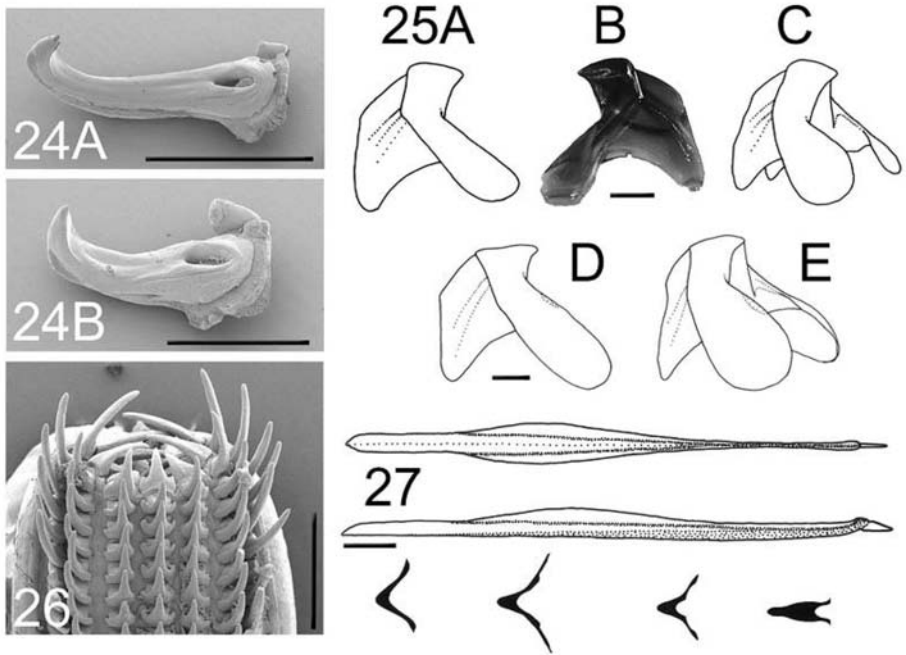


Figures 20–23. *Onychoteuthis compacta*. 20: distribution of Pacific specimens examined; grey circle indicates type locality. 21: USNM 813428, ML 89 mm, illustrations by K. H. Moore, scale bar = 10 mm. 22: right tentacular club, USNM 813395, ML 75 mm, scale bar = 1 mm. 23: left ventral tentacular hook series, USNM 813428, ML 89 mm, (A) dorsal profile, (B) oral view, scale bar = 1 mm

club, about four times longer than paired dorsal hooks and ~17% club length. Largest ventral hooks robust, with thick necks, curved in lateral profile; distal ventral hooks (V7–V10 or V11) with ventral basal cusp produced into spike (Fig. 24B) by ML 60 mm. Hook D2 largest in dorsal series; hook D5 smaller than hooks D1–D4 and slightly offset toward midline of club. Overall recurvature of hooks 70°–90°. Ventral club membrane ~30% club width along entire club length; dorsal membrane ~10% club width, flanking hooks D1–D4; dorsal keel ~75% club width, flanking dorsal hooks from D3 to club tip.

Lateral profile of lower beak (Fig. 25) longer than deep, with crest sloping steeply toward baseline (may have noticeable “hump” midway along its length in lateral profile (Figs. 25D,E), more commonly seen in female beaks), posterior edge of hood close to crest, hood length 50%–60% crest length, and hood and crest together 60%–70% baseline; jaw edge short, concave along entire length or concave distally and straight proximally; jaw angle obtuse, slightly obscured laterally by low, rounded, indistinct





Figures 24–27. *Onychoteuthis compacta*. 24: tentacular hooks, USNM 813428, ML 89 mm, (A) left tentacular hook V7, scale bar = 2 mm, (B) left tentacular hook V10, scale bar = 500  $\mu$ m. 25: lower beak, (A–C) KSB-013, ML 118 mm, (D), (E) USNM 813428, ML 89 mm, (A) left, (B) right, (C) left oblique profiles; (D) left profile, (E) left oblique, scale bars = 1 mm. 26: radula, KSB-013, ML 118 mm, scale bar = 500  $\mu$ m. 27: gladius, USNM 813428, ML 89 mm, scale bar = 10 mm

wing fold. Shoulder ridge distinct; angle ridge poorly developed, spanning ~50% lateral wall depth; angle point indistinct; distal wing width ~200% that at jaw angle, wing length 200%–230% LRL, with small triangular insert of cartilage below jaw angle; crest broad, slightly thickened; lateral wall diagonally bisected by dark, prominent ridge and fold, remaining distinct to lateral wall corner.

Radula (Fig. 26) with tricuspid rachidian, with narrow, conical mesocone and low, rounded lateral cusps 25%–30% mesocone height. First lateral tooth subequal to rachidian, with curved, slightly medially directed inner cusp, its outer cusp barely produced, shorter than lateral cusps of rachidian. Second lateral tooth simple, slightly curved, ~130% height of rachidian and first lateral. Marginal tooth simple, slightly curved, ~170% height of rachidian and first lateral. Palatine palp with ~27 mostly short, stubby teeth (with several longer, slender, curved teeth anteriorly), each 140–230% rachidian height, sparsely distributed over palp.

Gladius (Fig. 27) with greatest width (~7% GL) attained at ~35% GL; free rachis ~18% GL; vanes broaden and taper rapidly between 20% and 50% GL; dorsal keel solid, deep, comprising nearly entire gladius depth by ~70% GL. Rostrum ~5% GL, triangular in lateral profile, narrow, with nearly parallel margins in dorsal profile.

Overall coloration (preserved) pale creamy pink overlaid with dark reddish-brown chromatophores, darkest along visible ridge of gladius dorsally, becoming sparse but still distinct over dorsal and dorso-lateral mantle surfaces, small and nearly indistinguishable ventrally over anterior ~60% ML; large ventral unpigmented patch present over posterior ~40% ML (Fig. 21B). Dorsal and dorso-lateral surfaces of head dark

red-brown; lateral surfaces iridescent. Aboral surfaces of Arms I and II dark; Arms II with coppery-green iridescence over proximal 40% arm length; tentacle stalks with same iridescence ventral to aboral keel; chromatophores absent from oro-ventral tentacle stalk ridge and across oral face of stalk proximal to carpus (Fig. 59A).

*Remarks.*—*Onychoteuthis compacta* was described by Berry (1913) based on a juvenile of ML 21 mm. Due to paucity of material and the poor condition of the type (Fig. 3), this species was largely overlooked until Young and Harman (1987) attributed one of three paralarval Hawaiian *Onychoteuthis* to it. Kubodera et al. (1998) included it as a valid species, describing additional juvenile characters; Vecchione et al. (2003) added adult characters, including the unpigmented patch on the ventral mantle surface and the large basal spike on the distal-most ventral hooks. *Onychoteuthis compacta* is further described herein for biogeographic completeness, and to facilitate direct morphological comparison with other Pacific species.

The full depth distribution of *O. compacta* is unknown, although it occurs commonly at the surface at night.

### *Onychoteuthis borealijaponica* Okada, 1927

(Tables 4, 8, Figs. 28–36)

*Onychoteuthis borealijaponica* Okada, 1927: 4–7 — Okutani (1978): 144, 145 — Murata et al. (1982): 351–354 — Okutani and Murata (1983): 189–195 — Roper et al. (1984): 129 — Hess (1987): 290, 291, fig. 54d–i — Okutani et al. (1987): 114, 115, fig. 40 — Sweeney et al. (1992): 129, fig. 178 — Bigelow (1994): 13–23, tables 1–5, figs. 1–8 — Gillespie (1997): 15–20, tables 2, 3 — Kubodera et al. (1998): 279, fig. 2 — Sweeney and Roper (1998): 571 — Okutani (2005): 153 — Wakabayashi et al. (2007): 959–965, table 2, fig. 2.

*Onychoteuthis borealijaponicus* Okada, 1927 — Young (1972): 61–64, table 15, pl. 18A, 19A–G — Murata and Ishii (1977): 1–23 — Toll (1982): 55, 56, pl. 5B — Hess (1987): 290, 291, 300, 301, fig. 54d–i — Filippova et al. (1997): 180, figs. 106Γ [sic], E — Young and Harman (1998): 257–271, fig. 3b, table 1.

*Onychoteuthis banksii* (not Leach, 1817) — Berry (1916): 50 — Sasaki (1929): 228–230, pl. 20, fig. 12, pl. 30, figs. 1, 2 — Akimushkin (1965): 166–168, figs. 48, 49.

*Onychoteuthis boreali-japonicus* Okada, 1927 — Iverson and Pinkas (1971): fig. 37 — Clarke (1986): 72–74, fig. 32b.

*Onychoteuthis banksi borealijaponicus* Okada, 1927 — Nesis (1987): 192, 193, figs. 48D,E.

*Onychoteuthis banksi* (not Leach, 1817) — Filippova et al. (1997): Fig. 106B [sic].

*Distribution* (Fig. 28).—North Pacific (generally north of 30°N), 800–0 m, in the Kuroshio, Alaskan, and California currents, and the subtropical countercurrent. Elsewhere recorded from Aleutian Islands to Japan and southern Baja California (Nesis, 1987).

*Material Examined* (89 specimens).—NSMT Mo76092, ♀, ML 320 mm, off Sanriku coast [~40°01.6'N, 143°27.3'E], coll. M. Sato, Tohoku Fish Reg., NFD; CASIZ 057971, ♀, ML 270 mm, off entrance to Newport Bay, Orange County, California [~33°N, 117°W], coll. J.H. Souder, NFD; NSMT Mo66606 (5 sex indet.), ML 270–247 mm, 47°58.5'N, 174°59.7'E, 14/10/1985, RV No. 1 KANKI-MARU, gill net; NSMT Mo76091, ♀, ML 262 mm, off Sanriku coast [~40°01.6'N, 143°27.3'E], coll. M. Sato, Tohoku Fish Reg., NFD; USNM 1091107 (3 ♂), ML 262–244 mm, 50°00'N, 176°22'W, 15/08/1968, RV MILLER FREEMAN; USNM 000199, ♀, ML 245 mm, off salmon trawler, 11/07/1965,

Table 4. Measures (mm) and counts of *Onychoteuthis borealijaponica* Okada, 1927 (arm and tentacle measures recorded from more complete side of specimen, indicated R or L). See Table 1 for abbreviations.

Specimen ID	NSMT	NSMT	USNM	USNM	CASIZ	Mean indices	USNM	KSB-011	CASIZ	BMNH	Mean indices
Type Status	Mo76092	Mo76091	1091107	1091107	061056		727478		030508	20070547	
ML	None	262	244	245	None	(ML 123–320)	None	None	None	None	(ML 49–80)
Sex	F	F	M	M	F		M	F	F	Indet.	
MW	52	51	47	52	24	MWI	17	15	14	10	MWI
HL	35	38	51	38	21	HLI	11	18	12	9	HLI
HW	40	35	33	28	20	HWI	15	14	12	7	HWI
FL	170	140	142	137	73	FLI	45	38	37	26	FLI
FW	200	166	166	163	87	FWI	58	47	47	39	FWI
Arms I	81L	72L	102L	92L	38L	A1I	21R	20L	17L	14L	A1I
Arms II	95L	81L	107L	101L	48L	A2I	31R	27L	22L	16L	A2I
Arms III	93L	89L	108L	104L	48L	A3I	30R	27L	20L	16L	A3I
Arms IV	98L	81L	111L	105L	54L	A4I	31R	25L	23L	15L	A4I
TnL	166L	130L	265L	245L	88L	TnLI	37R	66L	30L	27L	TnLI
CL	64L	54L	66L	59L	32L	CLI	17R	18L	13L	12L	CLI
CS	10	7	9	9	9		9	10	9	7	
MH	27	25	26	25	26		23	25	25	26	
MS	0	0	0	0	0		0	0	0	0	
TPS	16	14	13	13	14		15	10	14	7*	

\* indicates damages features

\* indicates damages features

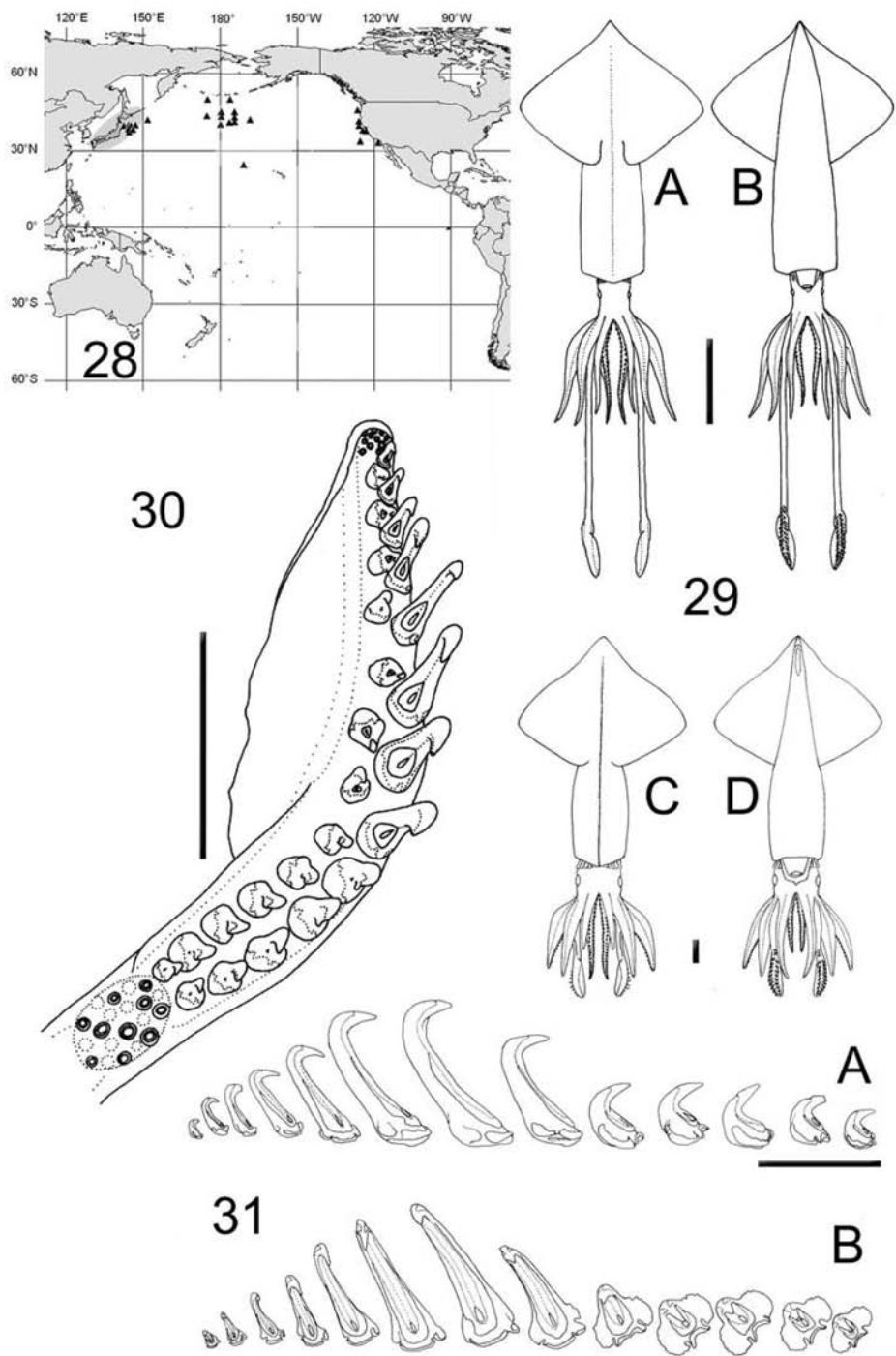
coll. D. Gotshall, Eureka Lab, A-125; NSMT Mo71957, ♀, ML 227 mm, 41°14.7'N, 143°39.9'E, off Sanriku, Japan, 550 m, 26/07/1996, RV MARUSADA-MARU, Dymo Stn 957, MWT; NSMT Mo74958, ♂, ML 220 mm, 40°01.6'N, 143°27.3'E, off Sanriku, Japan, 570 m, 13/07/1996, RV MARUSADA-MARU, Dymo Stn 1005, MWT; NSMT Mo74962, ♀, ML 202 mm, 41°17.7'N, 145°34.9'E, off Sanriku, Japan, 650 m, 22/07/1996, RV MARUSADA-MARU, Dymo Stn 1027, MWT; NSMT Mo74968, ♀, ML 200 mm, 41°10.2'N, 143°39.9'E, off Sanriku, Japan, 550 m, 26/07/1996, RV MARUSADA-MARU, Dymo Stn 1009, MWT; NSMT Mo74964, ♀, ML 200 mm, 41°17.7'N, 145°34.9'E, off Sanriku, Japan, 650 m, 22/07/1996, RV MARUSADA-MARU, Dymo Stn 1029, MWT; NSMT Mo71958, ♂, ML 190 mm, 41°14.7'N, 143°39.9'E, off Sanriku, Japan, 550 m, 26/07/1996, RV MARUSADA-MARU, Dymo Stn 958, MWT; NSMT Mo66909 (2 specimens), ♂, ML 190 mm, ♀, ML 183 mm, 38°22'N, 123°47'W, 17/09/[x], 2000 h, NFD; NSMT Mo74967, ♂, ML 185 mm, 41°17.7'N, 145°34.9'E, off Sanriku, Japan, 650 m, 22/07/1996, RV MARUSADA-MARU, Dymo Stn 1032, MWT; NSMT Mo74954, ♂, ML 178 mm, 41°19.6'N, 146°13.7'E, off Sanriku, Japan, 550 m, 09/07/1996, RV MARUSADA-MARU, Dymo Stn 1016, MWT; NSMT Mo74960, ♂, ML 175 mm, 40°59.7'N, 143°34.0'E, off Sanriku, Japan, 650 m, 20/07/1996, RV MARUSADA-MARU, Dymo Stn 975, MWT; NSMT Mo74963, ♂, ML 175 mm, 41°17.7'N, 145°34.9'E, off Sanriku, Japan, 650 m, 22/07/1996, RV MARUSADA-MARU, Dymo Stn 1028, MWT; KSB-045, ♂, ML 175 mm, 45°N, 174°30'W, 19/08/1991, TC 91-06, NMFS S-0281, squid jig; NSMT Mo74969, sex indet., ML 175 mm, 41°14.7'N, 143°39.9'E, off Sanriku, Japan, 550 m, 26/07/1996, RV MARUSADA-MARU, Dymo Stn 1049, MWT; NSMT Mo66890 (4 sex indet.), ML 173–131 mm, 37°00.5'N, 142°58.8'E, 1 m, 27/07/1972, 1000 h, RV Soyo-MARU Stn 1-7, HN; NSMT Mo72090, ♀, ML 170 mm, 40°01.0'N, 143°50.3'E, off Sanriku, Japan, 530 m, 13/07/1996, RV MARUSADA-MARU, Dymo Stn 945, MWT; NSMT Mo74966, ♂, ML 170 mm, 41°17.7'N, 145°34.9'E, off Sanriku, Japan, 650 m, 22/07/1996, RV MARUSADA-MARU, Dymo Stn 1031, MWT; NSMT Mo74956, ♂, ML 170 mm, 41°19.6'N, 146°13.7'E, off Sanriku, Japan, 550 m, 09/07/1996, RV MARUSADA-MARU, Dymo Stn 1018, MWT; KSB-044, ♀, ML 165 mm, 45°N, 179°30'W, 15/08/1991, TC 91-06, NMFS S-0280, squid jig; NSMT Mo71753, ♂, ML 163 mm, 40°00.1'N, 145°32.2'E, off Sanriku, Japan, 600 m, 14/07/1996, RV MARUSADA-MARU, Dymo Stn 942, MWT; NSMT Mo74957, ♀, ML 163 mm, 41°19.6'N, 146°13.7'E, off Sanriku, Japan, 550 m, 09/07/1996, RV MARUSADA-MARU, Dymo Stn 1019, MWT; NSMT Mo71783, ♂, ML 162 mm, 40°59.4'N, 144°44.0'E, off Sanriku, Japan, 550 m, 20/07/1996, RV MARUSADA-MARU, Dymo Stn 933, MWT; KSB-043, ♀, ML 158 mm, 45°01'N, 179°30'W, 14/08/1991, 2120–2220 h, TC 91-06 Stn 109, NMFS S0222; NSMT Mo74955, ♀, ML 152 mm, 41°19.6'N, 146°13.7'E, off Sanriku, Japan, 550 m, 09/07/1996, RV MARUSADA-MARU, Dymo Stn 1017, MWT; NSMT Mo72091, ♂, ML 150 mm, 40°01.0'N, 143°50.3'E, off Sanriku, Japan, 530 m, 13/07/1996, RV MARUSADA-MARU, Dymo Stn 946, MWT; NSMT Mo72017, ♀, ML 148 mm, 39°51.1'N, 143°27.4'E, off Sanriku, Japan, 650 m, 28/07/1996, RV MARUSADA-MARU, Dymo Stn 936, MWT; NSMT Mo66907 (2 specimens), ♂, ML 148 mm, ♀, ML 127 mm, 36°00'N, 125°35'W, 25/09/[x], NFD; NSMT Mo72089, ♀, ML 147 mm, 40°01.0'N, 143°50.3'E, off Sanriku, Japan, 530 m, 13/07/1996, RV MARUSADA-MARU, Dymo Stn 944, MWT; NSMT Mo74961, ♂, ML 145 mm, 40°59.7'N, 143°34.0'E, off Sanriku, Japan, 650 m, 20/07/1996, RV MARUSADA-MARU, Dymo Stn 976, MWT; NSMT Mo74965, ♂, ML 140 mm, 41°17.7'N, 145°34.9'E, off Sanriku, Japan, 650 m, 22/07/1996, RV MARUSADA-MARU, Dymo Stn 1030, MWT; NSMT Mo74959, ♀, ML 135 mm, 39°59.6'N,

143°32.6'E, off Sanriku, Japan, 530 m, 14/07/1996, RV MARUSADA-MARU, Dymo Stn 969, MWT; NSMT Mo71754, ♂, ML 135 mm, 40°00.1'N, 145°32.2'E, off Sanriku, Japan, 600 m, 14/07/1996, RV MARUSADA-MARU, Dymo Stn 943, MWT; CASIZ 061056, ♀, ML 123 mm, 36°46.4–47.0'N, 121°58.1–55.6'W, 648–504 m, 11/02/1975, Stn 38Ya, Tow 38, coll. M. E. Anderson; NSMT Mo66906 (2 specimens), ♀, ML 123 mm, ♂, ML 117 mm, 45°04.1'N, 175°00.7'E, 17/08/1985, RV KANKI-MARU, Stn 7, coll. T. Kubodera, gill net; NSMT Mo66905, ♀, ML 121 mm, 42°45'N, 153°43'E, 29/07/1972, 1900 h, No. 94; UMML 31.1305, ♀, ML 105 mm, 44°39'N, 125°17'W, off Oregon (State), 01/08/1961, coll. W. Pearcy; KSB-046, ♀, ML 104 mm, 41°03.5'N, 176°33.9'E, 150 m, 22/08/1983, 2133 h, CMT, coll. WMM and VAH, TC 83-03 Stn 10-2, NMFS-Ref S-0056; KSB-013, ♀, ML 92 mm, 24°36'N, 170°53.6'W, 93 km NW of Maro, 03/07/1990, TC 90-05 Stn 125; KSB-048, ♀, ML 83 mm, 41°58.8'N, 168°30.1'W, 50 m, 12/09/1983, 2012 h, CMT, coll. WMM and VAH, TC 83-03, NMFS-Ref S-0057; KSB-011 (6 sex indet.), ML 81–68 mm, 43°04'N, 179°30'W, 12/08/1991, 2215–2315 h, CMT, TC 91-06 Stn 85, NMFS S-0276; KSB-011 (8 specimens), 7 sex indet., ML 81–68 mm, ♀, ML 69 mm, 43°04'N, 179°30'W, 12/08/1991, 2215–2315 h, TC 91-06 Stn 85, CMT, NMFS S-0276; NSMT Mo71949, ♂, ML 80 mm, 41°21.2'N, 144°05.0'E, off Sanriku, Japan, 550 m, 25/07/1996, RV MARUSADA-MARU, MWT; USNM 727478, ♂, ML 80 mm, 33°15'N, 118°25'W, Southern California, 766 m, 22/10/1962, RV VELLERO IV 8237, 3 m IKMWT; KSB-053 (3 specimens), 2♀, ML 80, 79 mm, ♂, ML 74 mm, 45°00.2'N, 174°30.5'W, 158–0 m, 18/08/1991, 2042–2142 h, CMT, TC 91-06 Stn 135, NMFS S-0277; KSB-038 (4 sex indet.), ML 79–67 mm, 41°55.2'N, 168°29.4'W, 150 m, 12/09/1983, 2141 h, CMT, coll. WMM and VAH, TC 83-03 Stn 26-2, NMFS-Ref S-0050; KSB-054, ♂, ML 78 mm, 44°58'N, 174°35'W, 18/08/1991, 2216–2316 h, TC 91-06 Stn 136, NMFS S-0203; KSB-050, ♂, ML 75 mm, 40°06'N, 179°41'W, 08/08/1991, CMT, TC 91-06 Stn 39, NMFS S-0164; KSB-047, ♀ ML 75 mm, ♂ ML 71 mm, 43°00'N, 174°30'W, 142–0 m, 20/08/1991, 2054–2154 h, TC 91-06 Stn 159, NMFS S-0279; NSMT Mo66236 (2 ♀), ML 70, 67 mm, 38°N, 122°W, 14/07/1969, NFD; CASIZ 030508, ♀, ML 65 mm, Baja California, SW of Coronado Island [~32°40.68'N, 117°10.35'W], on surface, 03/07/1941, Stn 2561, coll. J.C. Marr; KSB-052, ♀, ML 63 mm, 41°14'N, 174°29'W, 500–0 m, 22/08/1991, 1610–1824 h, CMT, coll. KAB and J. Sinn; KSB-051, ♂ ML 59 mm, 43°12'N, 179°30'W, 12/08/1991, 1611–1837 h, CMT, TC 91-06 Stn 83, NMFS S-0177; BMNH 20070547 (3 sex indet.), ML 49, 37, 31 mm, California, 1962, coll. P. Foxton, NFD.

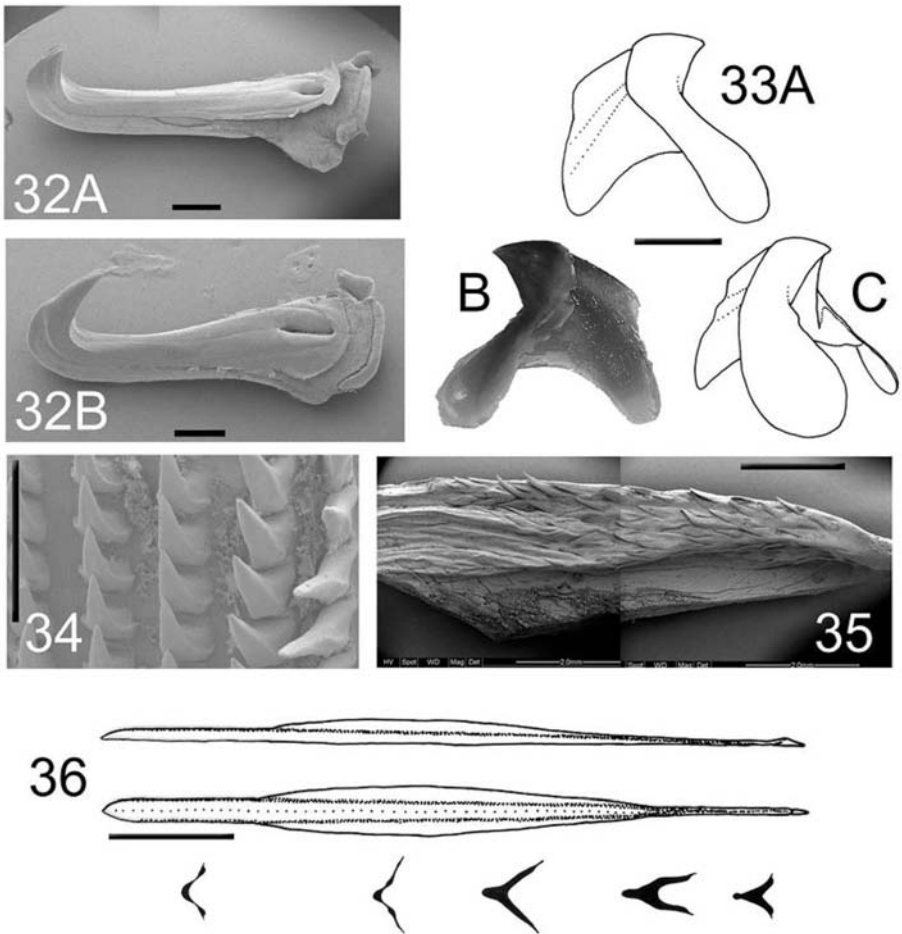
*Diagnosis.*—Both intestinal photophores always discernible, oval or tear-drop-shaped, anterior ~30% size of posterior, with somewhat indistinct edges, connected by a band of iridescent gold tissue; chromatophores absent from tentacle stalk proximal to carpus and along oro-ventral stalk ridge, but present over entire ventral surface of tail; tentacle club ~27% ML in subadults, ~21% ML in specimens of ML 70–80 mm, with 23–28 hooks; bases of distal-most ventral hooks with small ventral spike.

*Description* (Figs. 29–36).—Mantle muscular, smooth, slender, conical, width 18–21–25% ML; gladius visible dorsally as dark subcutaneous line; dorsal keel not protruding through mantle musculature; rostrum barely visible ventrally through distal ~3% ML; distal portion of mantle broadly attenuate; ventral surface of tail without apparent keel. Fins rhombic, length ~57% ML, width 62–69–75% ML, with large anterior lobes; posterior margins slightly concave medially, becoming convex laterally; anterior margins slightly convex. Intestinal photophores always discernible but with variably distinct margins, oval or tear-drop-shaped, each attenuated toward





Figures 28–31. *Onychoteuthis borealijaponica*. 28: distribution of specimens examined; grey oval indicates type locality. 29: (A, B) USNM 1091107, ML 244 mm, scale bar = 100 mm, (C, D): USNM 727478, ML 80 mm. 30: left tentacular club, NSMT Mo66905, ML 121 mm, scale bar = 10 mm. 31: left ventral tentacular hook series, USNM 1091107, ML 262 mm, (A) dorsal profile, (B) oral view, scale bar = 5 mm



Figures 32–36. *Onychoteuthis borealijaponica*, USNM 1091107, ML 262 mm. 32: tentacular hooks, (A) hook V7, scale bar = 1 mm, (B) hook V10, scale bar = 500  $\mu$ m. 33: lower beak, (A) left, (B) right, (C) left oblique profiles, scale bar = 5 mm. 34: radula, scale bar = 500  $\mu$ m. 35: right palatine palp, scale bar = 2 mm. 36: gladius, scale bar = 50 mm

the other; each approximately twice as long as wide; size of anterior  $\sim$ 30% that of posterior.

Head boxy, length 14–17–21% ML, width  $\sim$ 13% ML, depth  $\sim$ 11% ML; occipital region with seven to nine secondary folds. Funnel broad; aperture level with anterior margin of eye aperture; funnel groove shallow, well defined, V-shaped, extending to point directly below midpoint of eye. Ocular photophore elongate, rounded at both ends, uniformly broad, spanning ventral  $\sim$ 30% eye circumference. Mantle component of locking apparatus 20%–25% ML, funnel component  $\sim$ 12% ML.

Arms slender, 33–36<sub>I–IV</sub>–46% ML; formula II=III=IV>I; each with 90–100 suckers; oral faces of arms bordered on each side by low protective membrane with indistinct trabeculae; diameter of largest suckers 50%–60% arm width. Arms I without apparent keel; broad keels present on Arms II and III: that on Arms II  $\sim$ 100% arm depth to 40% arm length, narrowing thereafter to  $\sim$ 50% arm depth; that on Arms III  $\sim$ 150% arm depth by 40% arm length, thereafter  $\sim$ 100% arm depth to arm tip; lateral

membrane on Arms IV ~100% arm depth at base, gradually narrowing thereafter to ~40% arm width along remainder of arm.

Tentacles slender, 70–93–110% ML; stalk bases ~75% thickness of adjacent arms; aboral surface of stalk with small longitudinal keel. Clubs (Fig. 30) 24–27–31% ML (25%–40% TnL), only slightly expanded. Carpus ovoid, well defined, with seven to ten suckers (usually eight or nine); distal-most carpal suckers may crowd proximal hooks; manus with 23–27 robust hooks (Figs. 31, 32); terminal pad with ten to 16 suckers (usually 13–15). Bases of large ventral hooks asymmetrical, with those of hooks V7–V13 enlarged ventrally into small spike (Fig. 32B). Ventral hooks all larger than corresponding dorsal hooks, increasing in size through hook V7 or V8 (Fig. 32A); largest ventral hook about five times longer than corresponding dorsal hook and 16%–19% CL. Dorsal hooks decrease in size from D1 to D5, with D4 and D5 slightly offset toward centre of club; length of D6 subequal to D1, with hooks D7–D13 gradually decreasing in size distally. Ventral membrane ~80% club width, flanking hooks V1–V6; dorsal membrane ~20% club width, flanking hooks D1–D5; hooks D4–D13 bordered by dorsal keel, ~120% club width.

Lateral profile of lower beak (Fig. 33) longer than deep, with straight crest, sloping steeply downward, posterior edge of hood close to crest, hood length ~50% total crest length, and hood and crest together ~60% baseline; jaw edge weakly concave along entire length; jaw edge narrow and sharp; jaw angle obtuse, obscured by slight wing fold. Crest narrow, slightly thickened; lateral walls slightly indented below crest; shoulder ridge distinct, rounded; angle ridge distinct, spanning ~75% lateral wall depth; angle point distinct; wing width distally ~150% that at jaw angle, wing length ~250% LRL; small insert of clear cartilage present on medial wing margin just below jaw angle; lateral wall fold broad, rounded, well-developed anteriorly, becoming broader and shallower but still distinct to posterior margin of lateral wall.

Radula (Fig. 34) with unicuspid rachidian; mesocone robust, triangular, pointed distally; height of base ~20% height of rachidian; proximal margin of base straight, distal margin with distinct lateral corners. First lateral tooth unicuspid, subequal to rachidian, robust, forming nearly right triangle, with straight to slightly concave inner margin and straight to slightly convex outer margin. Second lateral tooth simple, robust, ~120% height of rachidian; margins of cusp straight to slightly convex. Marginal tooth simple, slender, with cusp somewhat twisted on some teeth; height ~180% that of rachidian. Palatine palp (Fig. 35) with ~65 large, flat, pointed teeth, each 150%–300% rachidian height, evenly set over surface of palp.

Gladius (Fig. 36) with greatest width (~7% GL) attained at ~40% GL; free rachis ~21% GL; vanes broaden and taper rapidly between 20 and 75% GL; dorsal keel robust, narrow; rostrum ~3% GL, triangular in lateral profile, narrow in dorsal profile.

Chromatophores present over entire ventral surface of tail, but not along oro-ventral tentacle stalk-ridge or across oral face of stalk, proximal to carpus.

Smaller specimens (below ML ~100 mm, Figs. 29C,D) deviate from the above description in having somewhat different body proportions: mantle slender, spindle-shaped, tapering rapidly beneath fins; fin width 68–73–80% ML; head length ~19% ML, width ~18% ML, depth ~14% ML; arm length 26–27–35<sub>II–IV</sub>–39% ML, each with 80–90 suckers bordered by trabeculate membrane; sucker diameter ~50% arm width on Arms I–III, ~30% arm width on Arms IV; keel on Arms II ~75% arm depth from ~20% arm length to arm tip; keel on Arms III ~120% arm depth by ~30% arm length, thereafter ~100% arm depth; lateral membrane on Arms IV ~150% arm width at

bases, narrowing thereafter to ~100% arm width over remaining arm length; tentacles robust, 46–61–95% ML, bases thicker than adjacent arms; club length ~23% ML (~45% TnL); adult club morphology present by ML 59 mm. Marginal suckers in paralarvae and small juveniles ovoid in outline, with small, proximally offset aperture (~25% sucker diameter); pegs with flattened oral faces, set in two concentric rows, polygonal in outline proximally, set in six to seven concentric rows and ovoid to round in outline distally; full series of marginal suckers present on club at ML 31 mm, with approximately half lost by ML 37 mm and all absent by ML 49 mm.

*Remarks.*—No type specimen was originally or has been subsequently designated for *O. borealijaponica* but the original description clearly describes the elongate photophores, contrasting them directly with the round photophores observed in *O. banksii*, and describes the band of iridescent tissue connecting the photophores, which Okada (1927) believed to be photogenic. Adam (1952) and Nesis (1987) considered *O. borealijaponica* to be a synonym and a subspecies of *O. banksii* respectively, but Young (1972) concluded that photophore shape, in addition to the number of hooks and the general robustness of the body, enabled differentiation of *O. borealijaponica* from *O. banksii* at ML > 12 mm.

*Onychoteuthis borealijaponica* is the largest known *Onychoteuthis* species, reaching ML > 350 mm. It is one of the few onychoteuthids fished commercially and as such, several studies have reported on aspects of its biology, growth and abundance (Okutani and Murata, 1983; Osako and Murata, 1983; Gillespie, 1997).

*Onychoteuthis meridiopacifica* Rancurel and Okutani, 1990

(Tables 5, 8, Figs. 37–45)

*Onychoteuthis* sp. Rancurel, 1970: 23–29, tables 6, 7, figs. 17, 18a, 19a — Nesis (1987): 193, fig. 48F — Okutani and Tsukada (1988): 19–21, table 5, figs. 10–12.

*Onychoteuthis meridiopacifica* Rancurel and Okutani, 1990: 25–30, figs. 1–7 — Kubodera et al. (1998): 280, fig. 4 — Sweeney and Roper (1998): 571 — Okutani (2005): 154.

*Distribution* (Fig. 37).—Southwest Pacific, off the eastern coast of Australia, 2000–0 m (based on three records; nearly all known specimens are ex-stomach-content), in the East Australian current. Elsewhere recorded from 15° to 30°S, 160°E to 170°W (Rancurel, 1970) and the northern Indian Ocean (Rancurel and Okutani, 1990).

*Material Examined* (65 specimens).—NMNZ M.172941 (2 specimens), ♀, ML 90 mm, ♂, ML 59 mm, 26°31.42'S, 166°34.42'E, NNW of Norfolk Island, 2000 m, 18/05/2003, RV TANGAROA, NORFANZ Stn 5; NMV F55013, ♂, ML 65 mm, 34°26.0'S, 151°25.0'E, 48 km east of Wollongong, Australia, 550–0 m, 25/03/1981, Engels high-lift demersal trawl, CSIRO RV SOELA; NSMT Mo76067 (6 specimens), ♂, ML 59 mm, 5 sex indet., ML 42–19 mm, 20°10.5'S, 153°20'E, 25/11/1975, RFRL RV Soyo-MARU Stn SP8; NMV F50968, ♀, ML 56 mm, 36°26–27'S, 151°24–23'E, 95 km east of Narooma, Australia, 600–475 m, 01/12/1978, EMWT 300, CSIRO RV COURAGEOUS; NSMT Mo76087 (2 specimens) ♂, ML 55 mm, ♀, ML 41 mm, 20°10.5'S, 153°20'E, 25/11/1975, RFRL RV Soyo-MARU Stn SP8; NSMT Mo76087 (2 specimens), ♂, ML 54 mm, ♀, ML 41 mm, 20°10.5'S, 153°20'E, 25/11/1975, RFRL RV Soyo-MARU Stn SP8; NSMT Mo76079, ♂, ML 54 mm, 19°56.8'S, 153°19.0'E, 30/11/1975, RFRL RV Soyo-MARU Stn SP42; NSMT Mo76085, ♂, ML 49 mm, 21°15'S, 155°11.5'E, 03/12/1975,





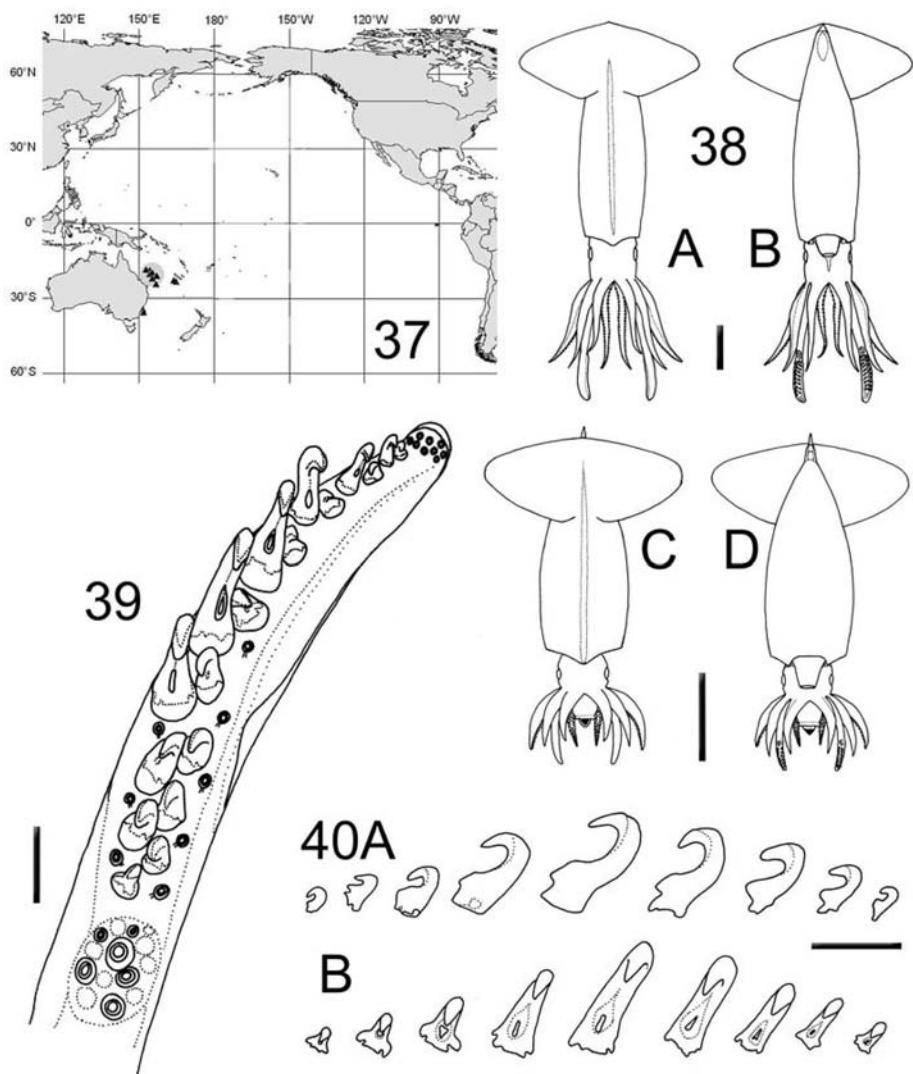
RFRL RV SOYO-MARU Stn SP131; NSMT Mo76059, ♀, ML 48 mm, 20°05'S, 153°14'E, 28/11/1975, RFRL RV SOYO-MARU Stn SP135, RFRL; NMNZ M.172966, ♂, ML 48 mm, 29°31.75'S, 167°38.05'E, Norfolk Ridge, 1200–200 m, 15/05/2003, RV TANGAROA, NORFANZ Stn 23; NSMT Mo76086 (6 sex indet.), ML 48–38 mm, 20°21.5'S, 154°14'E, 22/11/1975, RFRL RV SOYO-MARU Stn SP50; NSMT Mo76065 (2 ♀), ML 47, 42 mm, 21°23.5'S, 154°34'E, 01/12/1975, RFRL RV SOYO-MARU Stn SP37; NSMT Mo76082 (2 ♂), ML 47, 46 mm, 21°15'S, 155°11.5'E, 03/12/1975, RFRL RV SOYO-MARU Stn SP131; NSMT Mo76084 (5 sex indet.), ML 45–26 mm, 21°15'S, 155°11.5'E, 03/12/1975, RFRL RV SOYO-MARU Stn SP131; NSMT Mo76063, ♀, ML 44 mm, 20°21.5'S, 154°14'E, 22/11/1975, RFRL RV SOYO-MARU Stn SP54; NSMT Mo76066, ♂, ML 44 mm, 19°49.5'S, 153°01.5'E, 28/11/1975, RFRL RV SOYO-MARU Stn SP107; NSMT Mo76072, ♀, ML 44 mm, 20°25'S, 153°36'E, 30/11/1975, RFRL RV SOYO-MARU Stn SP5; NSMT Mo76080, sex indet., ML 38 mm, 19°49.5'S, 153°01.5'E, 28/11/1975, RFRL RV SOYO-MARU Stn SP106; NSMT Mo76081, ♀, ML 38 mm, 22°14.5'S, 156°24'E, 04/12/1975, RFRL RV SOYO-MARU Stn SP60; NSMT Mo76075 (2 specimens), ♀, ML 38 mm, ♂, ML 32 mm, 20°31.5'S, 155°44'E, 26/11/1975, RFRL RV SOYO-MARU Stn SP19; NSMT Mo76088 (4 sex indet.), ML 38–28 mm, 20°07.7'S, 154°05.5'E, 23/11/1975, RFRL RV SOYO-MARU Stn SP89; NSMT Mo76064 (7 sex indet.), ML 37–29 mm, 19°56.8'S, 153°19.0'E, 30/11/1975, RFRL RV SOYO-MARU Stn SP38; NSMT Mo76077, ♂, ML 36 mm, 20°42.2'S, 154°56.9'E, 03/12/1975, RFRL RV SOYO-MARU Stn SP95; NSMT Mo76070 (2 ♀), ML 35, 33 mm, 19°56.8'S, 153°19.0'E, 30/11/1975, RFRL RV SOYO-MARU Stn SP45; NSMT Mo76061 (6 sex indet.), ML 35–30 mm, 19°56.8'S, 153°19.0'E, 30/11/1975, RFRL RV SOYO-MARU Stn SP43; NSMT Mo76068, ♀, ML 33 mm, 20°16.1'S, 153°23.6'E, 26/11/1975, RFRL RV SOYO-MARU Stn SP103; NMNZ M.172989 (4 sex indet.), ML 26–16 mm, 29°31.75'S, 167°38.05'E, S of Norfolk Island, 1200–200 m, 15/05/2003, RV TANGAROA, NORFANZ Stn 23.

*Diagnosis.*—Fins very short, length ~40% ML; intestinal photophores tiny, may be poorly defined, with anterior only slightly smaller than posterior; chromatophores absent from tentacle stalk proximal to carpus; chromatophores present along oro-ventral stalk ridge; tentacle club length ~19% ML, with 15–19 short, robust hooks; distal-most ventral hook bases not produced into spike.

*Description* (Figs. 38–45).—Mantle muscular, spindle-shaped, width 21–26–32% ML; gladius visible dorsally as wide, rounded, amber-colored (in preserved specimens) ridge over anterior 85% ML; blunt rostrum visible ventrally through posterior ~5% ML; ventral mantle surface with fleshy oval pad over distal 15% ML, its width ~4% ML. Fins broadly rhombic, length 35–40–44% ML, width 69–80–90% ML; posterior and anterior margins straight; anterior lobes shallow, broadly rounded.

Head slightly narrower than mantle, length 14–18–22% ML, width ~19% ML, depth ~17% ML; dorsal and lateral surfaces convex, ventral surface flat; occipital region with eight small secondary folds. Funnel stout, with aperture level with midpoint of eyes; funnel groove well defined, V-shaped, broad posteriorly, attenuating anteriorly to narrow V, and reaching nearly to bases of Arms IV. Mantle component of locking apparatus ~40% ML, funnel component ~14% ML.

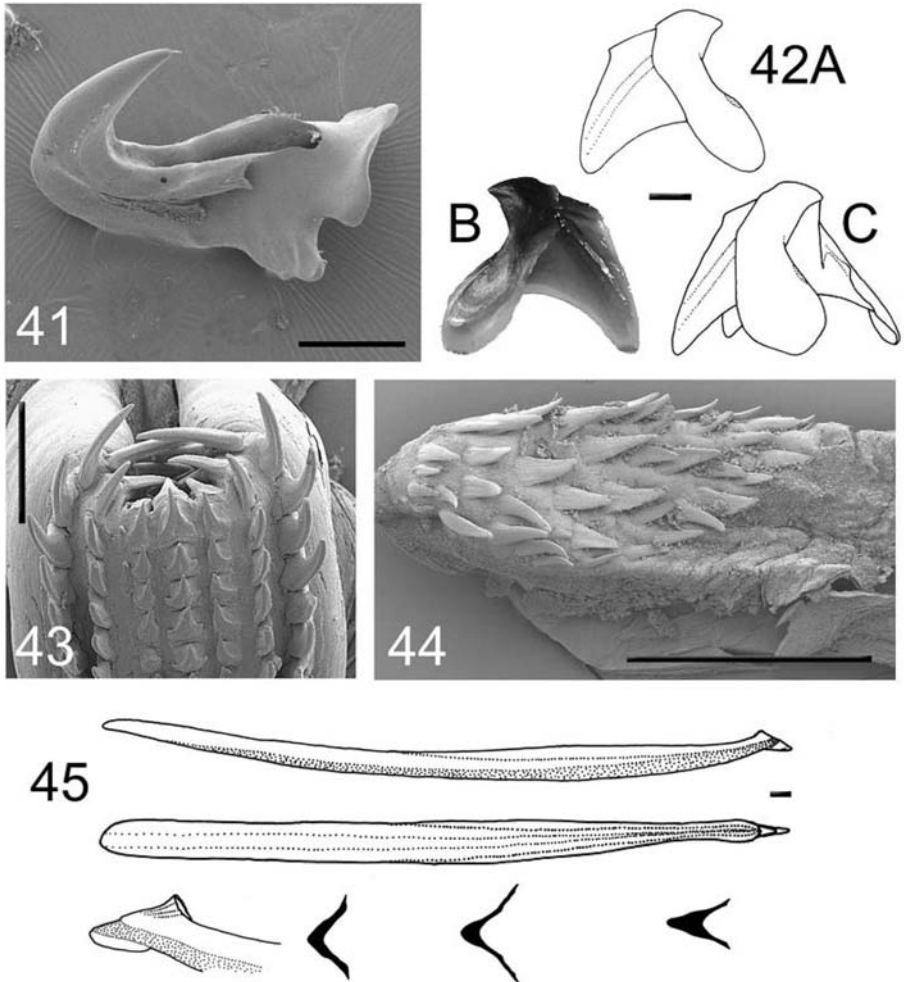
Arms 21–29<sub>I</sub>–34<sub>II–IV</sub>–44% ML, formula II=III=IV>I or III>IV>II>I, each with 50–60 suckers, diameter 40%–50% arm width, each with distal tissue produced into low fleshy knob; oral arm faces bordered on each side by low trabeculate membrane. Keels present on Arms I–III: those on Arms I and II ~10% arm width/depth along entire arm length; those on Arms III attaining 90% arm depth at 25% arm length,



Figures 37–40. *Onychoteuthis meridiopacifica*. 37: distribution of specimens examined; grey circle indicates type locality. 38: (A, B) NMNZ M.172941, ML 59 mm, (C, D) NMNZ M.172989, ML 26 mm, scale bars = 10 mm. 39, 40: NSMT Mo76059, ML 48 mm. 39: right tentacular club, scale bar = 1 mm. 40: right ventral tentacular hook series, (A) ventral profile, (B) oral view, scale bar = 1 mm

thereafter tapering to arm tips; Arms IV with lateral membrane 30% arm width over entire arm length.

Tentacles 40–51–67% ML; stalk bases narrower than adjacent arms. Clubs (Fig. 39) unexpanded to slightly expanded, length 16–19–22% ML (31%–42% TnL). Carpus squarish, with six to eight suckers; manus with 15–19 hooks (usually 17 or 18), with marginal suckers bordering proximal two to five hook pairs through at least ML 65 mm; terminal pad with seven to 11 suckers. Hooks (Figs. 40, 41) robust, close-set, with thick necks and long, strongly recurved claws. Proximal hook pair subequal in size, with ventral hook larger than paired dorsal hook in all subsequent pairs; hooks



Figures 41–45. *Onychoteuthis meridiopacifica*. 41: right tentacular hook V3, NMV F50968, ML 56 mm, scale bar = 200  $\mu$ m. 42–44: NMNZ M.172941, ML 90 mm. 42: lower beak, (A) left, (B) right, (C) left oblique profiles, scale bar = 1 mm. 43: radula, scale bar = 500  $\mu$ m. 44: right palatine palp, scale bar = 1 mm. 45: gladius, NSMT Mo76067, ML 59 mm, scale bar = 1 mm

D4 and D5 not markedly smaller or offset toward midline. Largest ventral hooks (V4 and V5) two to three times longer than paired dorsal hooks and ~16% CL; bases of largest ventral hooks slightly asymmetrical but lacking ventral spikes. Dorsal club membrane narrow, ~10% club width, bordering hooks D1–D3; ventral membrane scarcely evident, ~15% club width, extending along entire club length; dorsal keel ~80% club width, originating near hook D3 and continuing to club tip.

Lateral profile of lower beak (Fig. 42) longer than deep, with crest sloping gently toward baseline, domed hood, with posterior edge close to crest, hood length ~60% crest length, and hood and crest together ~60% baseline; jaw edge straight proximally, concave distally near rostral tip; jaw angle obtuse, slightly obscured by low, indistinct wing fold. Crest moderately broad; shoulder ridge distinct; angle ridge well developed but short, spanning ~40% lateral wall depth; angle point distinct, not

raised, darkly pigmented; distal wing width ~200% that at jaw angle, wing length ~200% LRL, with small insert of cartilage below jaw angle; lateral wall diagonally bisected by dark, prominent ridge and fold, remaining distinct to just above posterior corner of lateral wall.

Radula (Fig. 43) with tricuspid rachidian; mesocone triangular, slender distally; lateral cusps low, 15%–20% total rachidian height, slightly laterally directed. First lateral tooth subequal to rachidian, with single straight or slightly curved cusp oriented toward rachidian, with distal margin of base concave, forming small outer corner. Second lateral tooth simple, slightly curved, only slightly taller than rachidian. Marginal tooth simple, slightly curved, ~130% height of rachidian. Palatine palp (Fig. 44) with ~45 robust, flat teeth, each 130%–310% rachidian height; those near middle of palp largest, those near edges of palp more slender, curved outward away from surface of palp and set more densely.

Gladius (Fig. 45) with greatest width (~6% GL), attained at ~50% GL; free rachis ~40% GL; vanes broaden slightly between 40% and 50% GL, then taper gradually until 85% GL; dorsal keel comprises ~50% gladius depth at ~85% GL. Rostrum ~4% GL, stubby, triangular in lateral and ventral profiles, with conus recurved to form small, flared, pleated cup.

Overall coloration dark reddish-purple, darkest medially on dorsal surface of mantle, fins and head; lateral surfaces of mantle and head silvery to coppery iridescent. Arms and tentacles darkest aborally, paling laterally, palest on oral surfaces.

Smaller specimens (ML ~15–25 mm, Fig. 38C,D) deviate from the above description only in having somewhat different bodily proportions: mantle bulbous anterior to fins, width 35%–40% ML, thereafter tapering rapidly to form narrow tail pierced distally by rostrum of gladius; no fleshy ventral keel present; fins together ovate in outline, width ~90% ML, posterior margins forming nearly straight line across tail; head length, width and depth all ~20% ML; secondary occipital folds not developed, primary folds present; mantle component of locking apparatus ~46% ML, funnel component ~19% ML; buccal bulb protruding from arm crown; arm length 25%–35%, each with ~30 close-set suckers; aboral keels forming only on Arms III; tentacles slender, appearing flimsy, length ~35% ML; club length ~15% ML (~43% TnL); suckers and hooks damaged or absent in all specimens examined (sheaths present); one or two dark “tail spots” present beneath fins on either side of tail at ML 16–20 mm, but indistinct by ML 26 mm.

Spent female (ML 90 mm) with proportions similar to those of subadult and adult specimens as described above, but with tissues stretched, flabby; mid-portion of ventral mantle surface with two slightly diagonal longitudinal cuts, ~15% ML, nearly symmetrical across midline, each with 25–30 embedded spermatangia, anchored within mantle wall; tentacles absent (short stumps remaining).

*Remarks.*—Rancurel (1970) recognized *O. meridiopacifica* (his “*Onychoteuthis* sp.”) as distinct from *O. banksii* based on its small size at maturity and its broad, short fins. Additional distinctive character states include the small intestinal photophores, and robust tentacular hooks, lacking the more pronounced asymmetry and ventral spikes seen in congeners.

*Onychoteuthis lacrima* new species Bolstad and Seki

(Tables 6, 8, Figs. 46–54)

*Onychoteuthis* sp. (undescribed new species) — Bonnaud et al. (1998): 1761–1770, fig. 6.  
*Onychoteuthis* sp. D Seki, 2001: 44–50, figs. 14, 15.

*Distribution* (Fig. 46).—Shallow, north-central Pacific waters (200–0 m), primarily 30°–45°N and 170°W to 170°E; also found off eastern Japan.

*Type Material* (6 specimens).—SBMNH 423106, holotype, ♀, ML 94 mm, 37°59'N, 179°28'W, 154–0 m, 06/08/1991, 2142–2242 h, TC 91-06, Stn 15, CMT, NMFS S-0188, KSB-007; KSB-062 [USNM] (3 paratypes), ♀, ML 81 mm, 2 ♂, ML 73, 49 mm, TC 91-06 Stn 38, S-0171, NFD; SBMNH 423108, paratype, ♂, ML 72 mm, NW Hancock Seamount [~29°47'N, 179°04'E], 10/07/1983, TC 83-02, CMT, NMFS S-0528, KSB-009; SBMNH 423107, paratype, ♀, ML 54 mm, 37°59'N, 179°28'W, 154–0 m, 06/08/1991, 2142–2242 h, TC 91-06, Stn 15, CMT, NMFS S-0188, KSB-007.

*Additional Material Examined* (43 specimens).—NSMT Mo66608, ♂, ML 112 mm, 35°01.8'N, 174°58.7'E, 30/08/1985, Stn 27, hand-jig; KSB-049, ♀, ML 108 mm, 34°00.0'N, 177°30.5'E, 75 m, 26/08/1983, 2008 h, TC 83-03 Stn 14-1, CMT, coll. WMM and VAH, NMFS S-0042; KSB-036, ♀, ML 93 mm, 36°59'N, 179°29'W, 182–0 m, 05/08/1991, 2308–2358 h, TC 91-06 Stn 6, CMT, NMFS S-0161; NSMT Mo66887, ♀, ML 92 mm, 30°06'N, 142°11'E, 13/11/1971, 0130 h, RV SOYO-MARU Stn B6, coll. G. Honma; NSMT Mo66888, ♂, ML 91 mm, 29°00'N, 135°00'E, -/06/1969, NFD; NSMT Mo75319 (8 sex indet.), ML 91–38 mm, 40°01.3'N, 144°44.3'E, off Sanriku, Japan, 15 m, 16/07/1996, RV MARUSADA-MARU, MWT; KSB-040 (5 sex indet.), ML 89–70 mm, 37°23.0'N, 176°57.7'E, 150 m, 24/08/1983, 2200 h, TC 83-03 Stn 12-2, CMT, coll. WMM and VAH, NMFS S-0031; KSB-042 (8 sex indet.), ML 82–54 mm, 40°06'N, 179°41'W, 08/08/1991, TC 91-06 Stn 39, CMT, NMFS S-0164; KSB-034, ♂, ML 81 mm, 37°26.3'N, 177°01.5'E, 75 m, 24/08/1983, 2009 h, TC 83-03 Stn 12-1, CMT, coll. WMM and VAH, NMFS S-0051; KSB-039 (5 sex indet.), ML 81–53 mm, 33°56.5'N, 177°28.8'W, 150 m, 26/08/1983, 2140 h, TC 83-03 Stn 14-2, CMT, coll. WMM and VAH, NMFS S-0038; KSB-041 (4 sex indet.), ML 80–49 mm, TC 91-06 Stn 38, S-0171, NFD; NSMT Mo66701, ♀, ML 79 mm, 39°13.2'N, 147°08.7'E, 30/09/1988, 1800–1830 h, Stn SR-72; NSMT Mo66883, ♀, ML 76 mm, 34°58.8'N, 157°06.8'E, surface, 21/05/1972, 2010–2039 h, RV SOYO-MARU Stn 78, HN; NSMT Mo66889 (4 sex indet.), ML 76–63 mm, 37°00.5'N, 142°58.8'E, 1 m, 27/07/1972, 1000 h, RV SOYO-MARU Stn 1-7, HN; NSMT Mo75326, sex indet., ML 46 mm, 39°00.6'N, 143°32.1'E, off Sanriku, Japan, 650 m, 29/07/1996, RV MARUSADA-MARU, MWT.

*Diagnosis*.—Posterior intestinal photophore oval or tear-drop-shaped, usually well defined; anterior intestinal photophore circular, minute, ill-defined and occasionally indiscernible; chromatophores absent from tentacle stalk proximal to carpus and along oro-ventral stalk ridge, but present over entire ventral surface of mantle; tentacle club 26%–32% ML, with 20–24 long, slender hooks; distal-most ventral hooks with large, ventral, oro-laterally directed basal spike.

*Description* (Figs. 47–54).—Mantle anteriorly cylindrical, width 19–21–25% ML; keel of gladius raised through dorsal midline, forming dark ridge; rostrum of gladius visible ventrally through distal ~5% ML; mantle robust distally, with small fleshy keel, ~15% ML. Posterior intestinal photophore oval or tear-drop-shaped, occasionally with indistinct borders; anterior intestinal photophore greatly reduced, generally





circular in outline but often indistinct and occasionally indiscernible. Fins rhombic, length generally 54–58–61% ML, width 69–73–84% at ML > 70 mm, broader at ML 49–69 mm, occasionally 85–90% ML; posterior margins straight to slightly concave distally, anterior margins gently convex; lateral “corners” sharp; anterior lobes small, rounded.

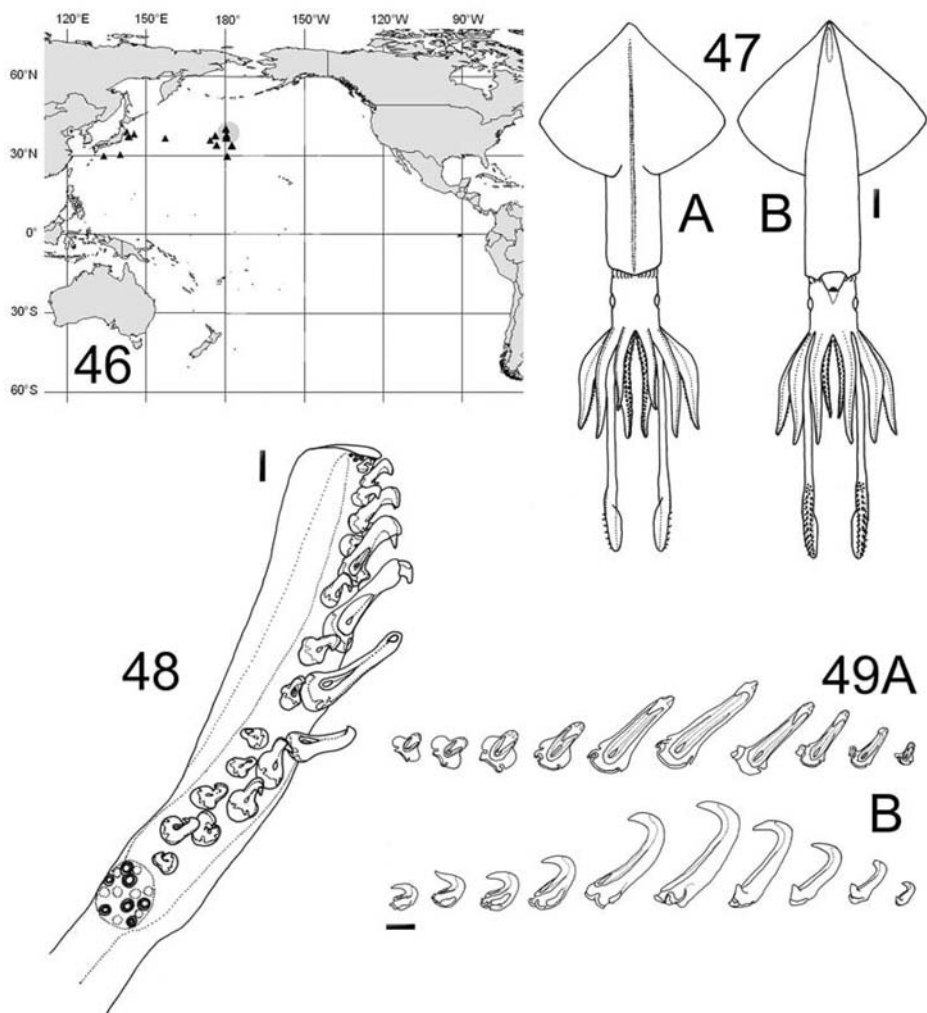
Head cylindrical, length 15–24–32% ML, width 16–20–25% ML; depth ~16% ML; not constricted anterior to brachial crown; occipital region with seven to nine secondary folds. Funnel groove V-shaped, broad posteriorly, becoming acute anteriorly, reaching to point directly below midpoint of eyes. Ocular photophore broad, rounded anteriorly, tapering to narrow point posteriorly, spanning ventral ~40% eye circumference. Funnel component of locking apparatus 13%–21% ML; mantle component 26%–32% ML.

Arms muscular, 27–32–43<sub>I–IV</sub>–48% ML, formula II=III=IV>I; each with 80–90 suckers (~60 at ML 49 mm), each with a small fleshy distal knob. Aboral keels present on Arms I–III: that on Arms I ~10% arm width along entire arm length; that on Arms II ~30% arm depth along entire arm length; that on Arms III ~130% arm depth at ~40% arm length, narrowing thereafter; lateral membrane on Arms IV ~100% arm width along entire arm length.

Tentacles robust, length 72–88–128% ML; stalk bases comparably thick to adjacent arms; aboral surface of stalk with low keel, ~10% stalk thickness. Club (Fig. 48) slightly expanded, length 26–29–32% ML (24%–38% TnL); carpus circular to slightly ovoid in outline, with 7 to 10 suckers (usually 9); manus with 20–24 hooks (usually 21 or 22) (Figs. 49, 50); terminal pad with 12–16 suckers (usually 13 or 14). Hooks D1 and D2 subequal to paired ventral hooks; dorsal hooks diminish in size thereafter through hook D5 or D6, with D4 and D5 (or D5 and D6) slightly off-set toward centre of club; hook D6 or D7 suddenly enlarged (similar in size to proximal-most dorsal hooks), with dorsal hooks thereafter decreasing in size distally. Largest ventral hooks (V6–V8) (Fig. 50A) with slightly curved necks and acutely recurved claws (80°–90°) in lateral profile; longest hook 18%–25% club length (average 20%) and four to six times longer than paired dorsal hook; hooks V7 or V8 through distal-most ventral hook with large, oro-laterally directed spike on ventral side of hook base (Fig. 50B). Ventral club membrane ~50% club width along hooks V1–V5, narrowing thereafter to ~10% club width along remainder of club length; dorsal membrane ~30% club width, flanking hooks D1–D4; dorsal keel ~100% club width, from hook D2 or D3 through tip of club.

Lateral profile of lower beak (Fig. 51) longer than deep, with crest sloping steeply toward baseline, posterior edge of hood well above crest, hood length ~45% total crest length, and hood and crest together ~80% baseline; jaw edge straight proximally, with rostrum produced into sharp or slightly rounded tip; jaw angle obtuse, not obscured laterally by wing fold; shoulder ridge sharp. Crest narrow, rounded, slightly thickened; lateral walls slightly indented between crest and lateral wall fold; angle ridge well defined but short, spanning ~50% lateral wall depth; distal wing width ~120% that at jaw angle, wing length ~200% LRL, with small triangular insert of cartilage below jaw angle; lateral wall diagonally bisected by dark, prominent ridge and fold, remaining distinct to lateral wall corner.

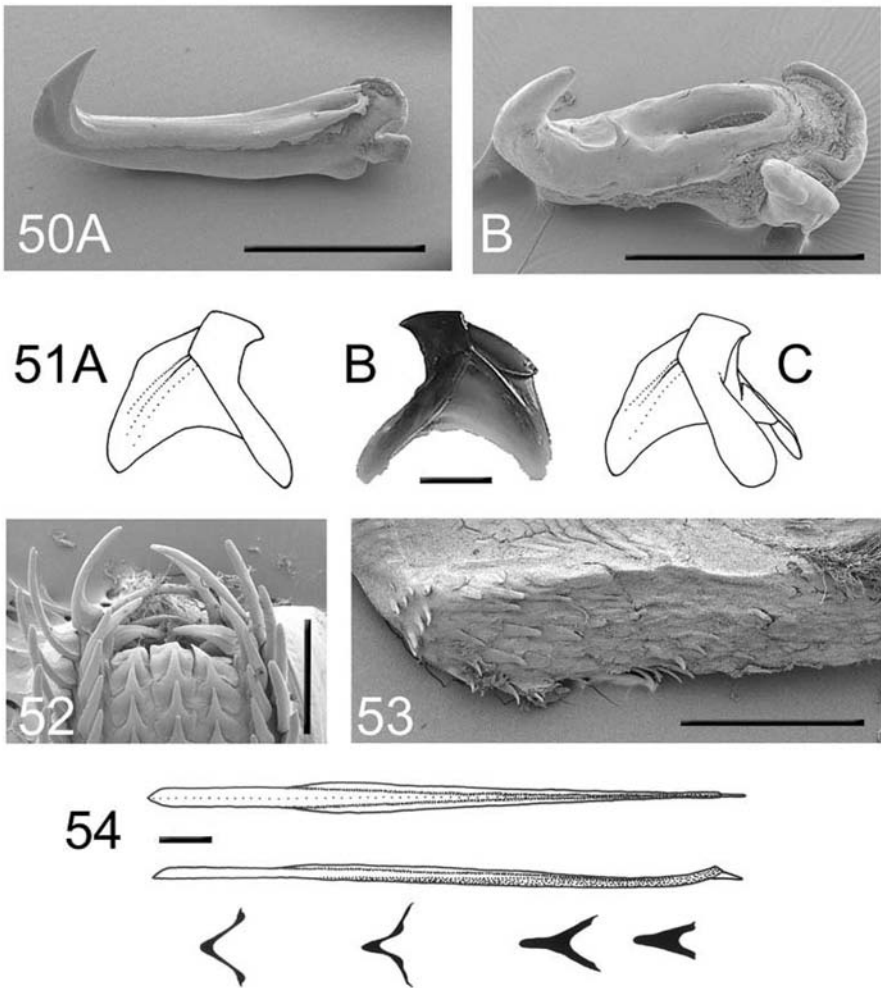
Radula (Fig. 52) with slightly tricuspid rachidian, with short, narrow, triangular mesocone and narrow, rounded, slightly laterally directed lateral cusps, their height ~40% that of mesocone height. First lateral tooth unicuspid, straight, slightly shorter



Figures 46–49. *Onychoteuthis lacrima* sp. nov. 46: distribution of specimens examined; grey circle indicates type locality. 47: holotype, SBMNH 423106, ML 94 mm, scale bar = 10 mm. 48: left tentacular club, paratype, SBMNH 423108, ML 72 mm, scale bar = 1 mm. 49: right ventral tentacular hook series, paratype, KSB-062 [USNM], ML 81 mm, (A) oral view, (B) ventral profile, scale bar = 1 mm

than rachidian and of similar breadth, with base shorter on inner edge of tooth than outer, with margins of base often indistinguishable from margins of cusp. Second lateral tooth simple, robust, straight, short, ~120% rachidian height. Marginal tooth simple, curved, ~250% rachidian height. Palatine palp (Fig. 53) with ~65 short, flat, poorly defined teeth, each 70%–160% rachidian height, curving slightly away from surface of palp, densely distributed over palp.

Gladius (Fig. 54) with greatest width (~5% GL) attained at ~35% GL; free rachis ~23% GL; vanes broaden rapidly from 25% to 35% GL, then taper gradually until 85% GL; dorsal keel solid, deep, comprising nearly entire gladius depth by ~70% GL. Conus (including rostrum) ~4% GL; rostrum triangular in lateral profile, narrow in dorsal profile.



Figures 50–54. *Onychoteuthis lacrima* sp. nov., paratype, KSB-062 [USNM], ML 81 mm. 50: right tentacular hook, (A) hook V6, scale bar = 2 mm, (B) hook V10, scale bar = 500  $\mu$ m. 51: lower beak, (A) left, (B) right, (C) left oblique profiles, scale bar = 1 mm. 52: radula, scale bar = 500  $\mu$ m. 53: palatine palp, scale bar = 1 mm. 54: gladius, scale bar = 10 mm

*Etymology*.—The name *lacrima* (Latin for “tear” or “tear drop”) is given to this species based on the distinctive shape of the posterior visceral photophore.

*Remarks*.—The paralarva of *O. lacrima* sp. nov. was described and illustrated by Seki (2001, “sp. D”), based on character states (most obviously the absence of chromatophores on the posterior ventral region (“belly”) of the mantle) that distinguished it from paralarvae of three other *Onychoteuthis* species then recognized from Hawaiian waters — *O. compacta*, *O. spp. B* and *C* — by Young and Harman (1987). Ontogenetic series of specimens attributed to sp. D can be tracked from paralarval to subadult stages, characterized by the absent or minute anterior intestinal photophore and oval posterior intestinal photophore, and the presence of chromatophores over the entire ventral mantle surface. Of locally occurring congeners, *O. lacrima* sp. nov. is most similar to *O. aequimanus* and *O. borealijaponica*, but it is readily

separable from the former by the shape and size of the intestinal photophores and by the presence of large ventral basal spikes on the distal-most ventral tentacular hooks, and generally from the latter by the number of tentacular hooks. The full complement of tentacular hooks has earlier been described for this species by ML 70 mm (Seki, 2001), but herein is reported for specimens by ML 49 mm.

All available material has been collected from a relatively small area within the North Pacific Transition Zone (approximately 30°–40°N and 170°E–170°W, Fig. 46), and off Japan. The distribution of *O. lacrima* sp. nov. thus overlaps with that of *O. borealijaponica* (Fig. 28) and *O. compacta* (Fig. 20), but not that currently recognized for *O. aequimanus* (Fig. 13).

*Onychoteuthis lacrima* sp. nov. was included in Bonnaud et al.'s (1998) phylogenetic study of the Onychoteuthidae, as "*Onychoteuthis* sp. (undescribed new species)" (R. Young, University of Hawaii, pers. comm.). It appeared less closely related to *O. compacta* and *O. prolata* sp. nov. than the latter two were to each other.

### ***Onychoteuthis prolata* new species Bolstad, Vecchione, and Young**

(Tables 7, 8, Figs. 55–63)

? *Onychoteuthis* sp. B Young and Harman, 1987 — 313–321, figs. 1–4, 7, tables 1–3 — Sweeney et al. (1992): 129, fig. 180 — Bonnaud et al. (1998): 1761–1770, fig. 6 — Seki (2001): 44–50.

*Pacific Distribution* (Fig. 55).—shallow Hawaiian waters (200–0 m), in the Subtropical Countercurrent, and one record near the equator, at 139°W. Rare in collections but appears to occur worldwide in temperate and tropical oceans, 1300–0 m.

*Type Material* (2 specimens).—SBMNH 423101, holotype, ♀, ML 135 mm, off Kona Coast of Hawaii [~19°38.6'N, 159°59.39'W], surface, 10/09/1980, 0145 h, RV KANA KEOKI, dipnet, KSB-001; USNM 1102755, paratype, ♀, ML 155 mm, Honolulu, HI, 19632, Stn CHG-7, coll. C. Gilbert, NFD.

*Additional Material Examined* (11 specimens).—USNM 813418, ♀, ML 127 mm, 00°52'S, 139°52'W, 200–0 m, 25/09/1956, RV H.M. SMITH, NL&D; KSB-003, ♂, ML 123 mm, off Kauai [~22°10'N, 159°30'W], -/05/2000, coll. W. Ishikawa; SAM S299 (2 ♀), ML 109, 91 mm, 23°20'S, 53°56'E, 02/12/1975, coll. P. Best, squid jig; UMML 31.92, ♂, ML 101 mm, Key Biscayne, Florida [~25°41'N, 80°09'W], 10/03/1957, coll. J. Gill; KSB-002, ♀, ML 110 mm, TC-52-15, NFD; MNHN 637, ♀, ML 83 mm, Bahia, Brazil [~15°S, 38°W], 1844, coll. Lemesle, NFD; BMNH 20070532, ♀, ML 78 mm, 18°27'S, 03°29'E, 12/06/1937, "Discovery" Expedition, on deck; D1159 XI, sex indet., ML 76 mm, 17°55'N, 24°35'W, surface, 30/10/1921, 0145 h, Dana Expedition Stn 1159 IX; UMML 31.1513, sex indet., ML 71 mm, 29°27'–25'N, 70°08'–09'W, surface, 06/08/1964, RV PILLSBURY Stn 161; UMML 31.2959, ♀, ML 59 mm, 13°36'N, 60°45'W, 1298 m, 09/03/1966, RV OREGON Stn 5953.

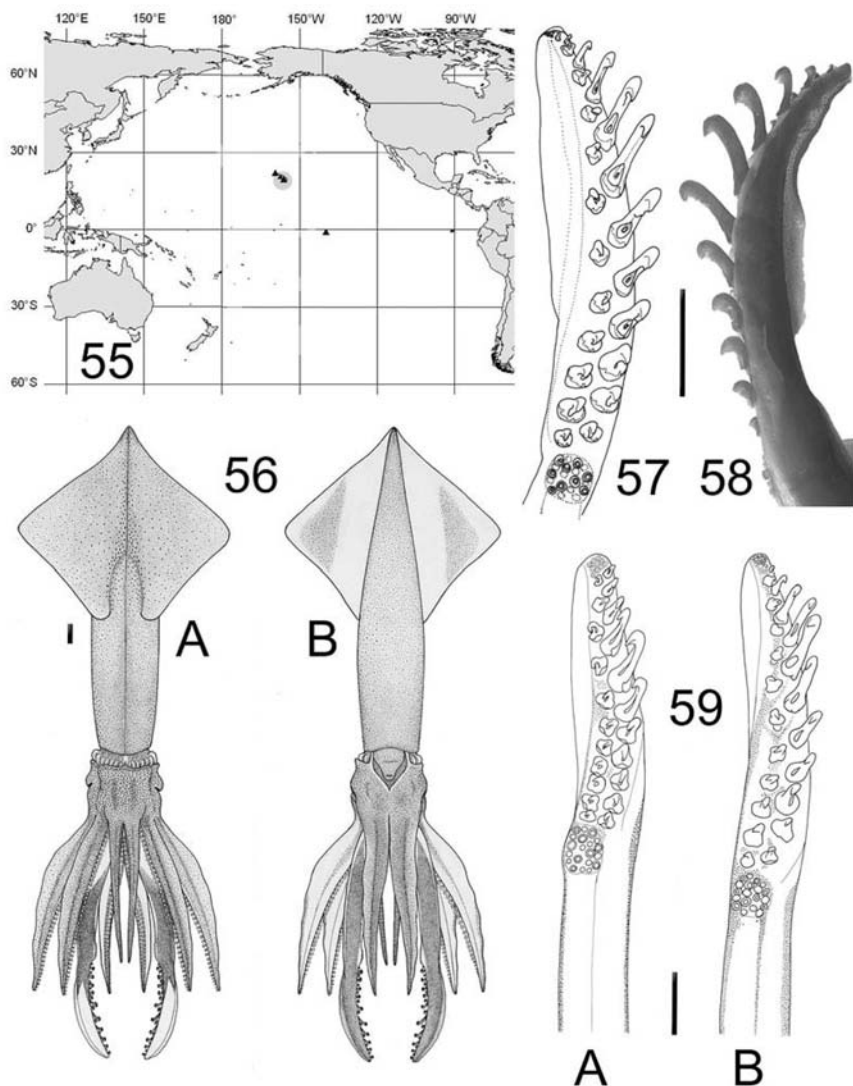
*Diagnosis*.—Intestinal photophores circular, well defined, diameter of anterior 50%–75% that of posterior; chromatophores present on tentacle stalk proximal to carpus and along oro-ventral stalk ridge, and over entire ventral surface of tail; tentacle club ~36% ML, with 20–23 long, sharply recurved hooks, without ventral basal spikes in distal-most ventral hooks.

*Description* (Figs. 56–63).—Mantle muscular, width 18–22–27% ML; gladius visible dorsally as dark line, but keel does not protrude above dorsal mantle surface;



Table 7. Measures (mm) and counts of *Onychoteuthis prolata* sp. nov. (arm and tentacle measures recorded from more complete side of specimen, indicated R or L). See Table 1 for abbreviations.

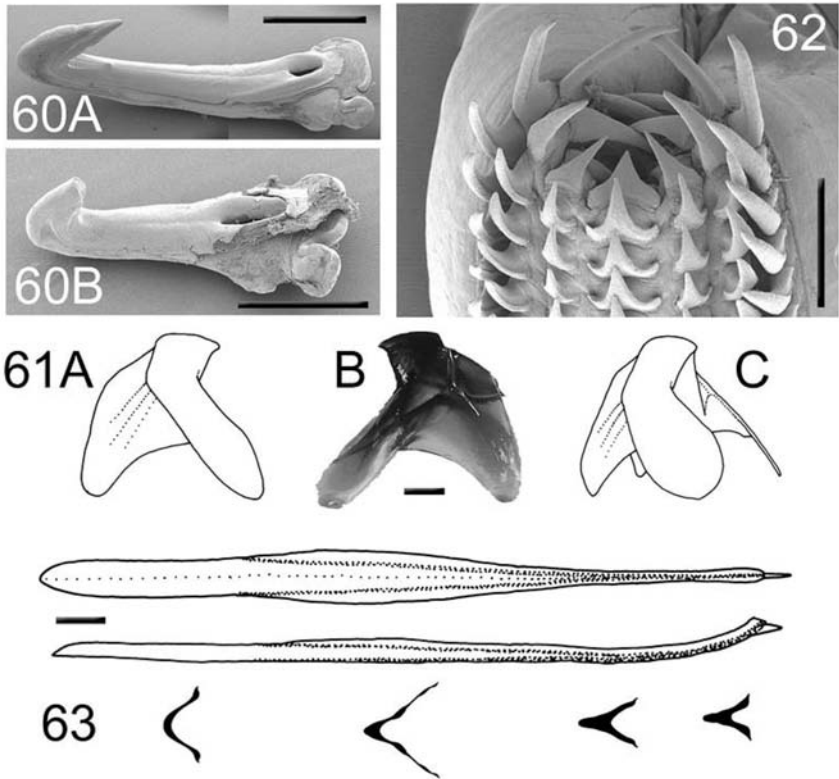
Specimen ID	SBMNH 423101	USNM 1102755	USNM 813418	KSB-003	KSB-002	UMML 31.92	Dana 1159IX	UMML 31.1513	UMML 31.2959	Mean indices
Type Status	Holotype	Paratype	None	None	None	None	None	None	None	
ML	135	155	127	123	110	101	76	71	59	(ML 59–155)
Sex	F	F	F	M	F	M	Indet.	Indet.	F	
MW	28	28	32	26	28	21	14	19	13	MW1 22
HL	33	24	28	22	25	25	17	17	11	HL1 21
HW	27	23	17	22	20	20	15	12	9	HW1 17
FL	81	93	80	76	64	63	45	41	32	FL1 60
FW	89	95	85	86	66	75	57	52	41	FW1 68
Arms I	53L	78L	71L	60L	51R	46L	31L	29R	24L	A1I 45
Arms II	68L	98L	76L	79L	61R	59L	40L	35R	31L	A2I 56
Arms III	69L	95L	70L	76L	59R	60L	39L	35R	31L	A3I 55
Arms IV	71L	93L	80L	81L	61R	57L	42L	31R	32L	A4I 56
TnL	98L	153L	154L	147L	115R	94L	83L	69R	65L	TnL1 103
CL	54L	61L	52L	46L	31R	37L	27L	23R	22L	CL1 36
CS	9	8	8	9	8L	8	7	8	7	
MH	23	22	22	23	22L	22	23	22	20	
MS	0	0	0	0	0L	0	0	0	0	
TPS	13	14	16	18	14L	12	16	13	13	



Figures 55–59. *Onychoteuthis prolata* sp. nov. 55: distribution of specimens examined; grey circle indicates type locality. 56–58, 59B: holotype, SBMNH 423101, ML 135 mm. 56: illustrations by K. H. Moore, scale bar = 10 mm. 57: left tentacular club, oral view, 58: left tentacular club, ventral view, scale bar = 10 mm. 59: chromatophore patterns on tentacular clubs of (A) *Onychoteuthis compacta*, USNM 813428, ML 89 mm; (B) *O. prolata* sp. nov., scale bar = 10 mm

rostrum of gladius visible ventrally through distal ~10% ML; mantle robust distally, without apparent fleshy ventral keel. Intestinal photophores circular, well defined, diameter of anterior 50%–75% that of posterior. Fins large, rhombic, length 54–60–63% ML, width 60–68–75% ML; posterior margins straight, becoming slightly concave distally; anterior margins varying from slightly convex to slightly concave, lateral “corners” sharp, forming approximate right angle.

Head approximately cylindrical, length 15–21–25% ML, width 13–17–20% ML, depth 11%–19% ML, widening slightly proximal to arm bases; occipital region with



Figures 60–63. *Onychoteuthis prolata* sp. nov. 60: holotype, SBMNH 423101, ML 135 mm, (A) right ventral hook V7, (B) right ventral hook V11, scale bars = 2 mm. 61, 62: KSB-003, ML 123 mm. 61: lower beak, (A) left, (B) right, (C) left oblique profiles, scale bar = 1 mm. 62: radula, scale bar = 1 mm. 63: gladius, USNM 1102755, paratype, ML 155 mm, scale bar = 10 mm

seven to nine secondary folds; funnel groove well defined, triangular, narrowing to acute anterior point level below midpoint of eyes. Ocular photophore broad, rounded at both ends and of uniform breadth along its length, spanning ventral ~50% eye circumference. Funnel component of locking apparatus 11%–15% ML; mantle component 21%–28% ML.

Arms slender,  $39\text{--}45\text{--}56_{\text{I--IV}}$ –66% ML, formula  $\text{II}=\text{III}=\text{IV}>\text{I}$ , attenuating to narrow tips; suckers on each arm number 90–100 and generally lack distal fleshy knobs; sucker diameter ~50% arm width on Arms I–III, ~40% arm width on Arms IV. Keels present on Arms I–III: that on Arms I ~5% arm width along entire arm length; that on Arms II ~50% arm depth along entire arm length; that on Arms III ~150% arm depth at ~40% arm length, narrowing distally; lateral membrane on Arms IV ~100% arm width at base, narrowing thereafter to ~75% arm width along remainder of arm length.

Tentacles robust, length 73–103–121% ML; thickness of stalk at base comparable to that of adjacent arms; aboral keel ~10% stalk thickness proximally, widening to 20% distally. Club (Figs. 57, 58, 59B) 28–36–40% ML (27%–55% TnL), expanded; carpus broad, ovoid, with seven to nine suckers; manus with 20–23 long, robust, widely spaced hooks, with V5 or V6 longest (Fig. 60A, three to five times longer than paired dorsal hook and 16%–21% CL); terminal pad with 12–18 suckers. Largest ventral

hooks slender, with nearly straight necks and acutely recurved claws in lateral profile; ventral bases of distal-most ventral hooks not produced into spike (Fig. 60B).

Lateral profile of lower beak (Fig. 61) longer than deep, with crest sloping steeply toward baseline, posterior edge of hood well above crest, hood length ~50% total crest length and hood and crest together ~65% baseline; jaw edge short, slightly concave along entire length; jaw angle obtuse, slightly obscured by low, rounded wing fold. Crest broad, rounded, slightly thickened; lateral wall not indented between crest and lateral wall fold; shoulder ridge rounded; angle ridge well defined but short, spanning ~40% lateral wall depth; angle point indistinct; distal wing width ~200% that at jaw angle, wing length 275%–300% LRL, with small triangular insert of cartilage below jaw angle; lateral wall diagonally bisected by dark, prominent ridge and fold, becoming indistinct by lateral wall corner.

Radula (Fig. 62) with tricuspid rachidian, with broad triangular mesocone and narrow, rounded, slightly laterally directed lateral cusps, their height ~30% of total rachidian height. First lateral tooth bicuspid, inner cusp straight or slightly curved, subequal or slightly shorter than rachidian and slightly narrower, medially directed; outer cusp low, rounded, slightly laterally directed. Second lateral tooth simple, robust, curved, ~150% height of rachidian. Marginal tooth simple, curved, ~180% rachidian height. Palatine palp not examined due to limited material.








Gladius (Fig. 63) with greatest width (~7% GL) attained at ~40% GL; free rachis ~27% GL; vanes broaden and taper rapidly between 30% and 65% GL; dorsal keel robust, narrow. Rostrum short, ~4% GL; rostrum triangular in lateral profile, narrow in dorsal profile.

Overall coloration (preserved) pale pink overlaid with dark purplish-brown chromatophores, darkest along dorsal midline, becoming sparse but still distinct over dorsal and dorso-lateral mantle surfaces and dorsal surface of fins, fine but distinct over entire ventral mantle surface. Dorsal and dorso-lateral surfaces of head purple; lateral and ventral surfaces iridescent. Aboral surfaces of arms pinkish-purple, slightly iridescent; tentacle stalks with same iridescence ventral to aboral keel; chromatophores present proximal to carpus (Fig. 59B) in band from oro-ventral tentacle stalk ridge and across oral face of stalk proximal to carpus, and along oro-ventral stalk ridge.

*Remarks.*—The overall appearance of this species is quite robust, and the long, broad tentacle clubs with their large, widely spaced, strongly recurved hooks (Figs. 58, 60) are its most distinctive characters. Of all congeners, *O. aequimanus* is the most similar, although *O. aequimanus* appears more slight of body, its tentacular clubs are generally shorter, and its hooks are more slender and less recurved.

Genetic material from Young and Harman's (1987) "species B" paralarvae (herein tentatively attributed to *O. prolata* sp. nov.) was also included by Bonnaud et al. (1998) in their phylogenetic study of the Onychoteuthidae, as "*Onychoteuthis* sp. B" (R. Young, University of Hawaii, pers. comm.), where it was found to be closely related to *O. compacta* and somewhat more distantly to *O. lacrima* sp. nov.

Table 8. Subadult to adult characters/states in all Pacific species of *Onychoteuthis* Lichtenstein, 1818, with *O. banksii* included for reference. ML = dorsal mantle length.

Character species	Visceral photophores	Ocular photophore	Club length as % ML	Number of manus hooks	Spike on distal most ventral hooks	Chromatophores along oro-ventral tentacle stalk ridge	Chromatophore band proximal to carpus	Chromatophores on postero-ventral mantle margin
<i>O. banksii</i>		Uniformly broad, spans ventral ~30% eye circumference	21–38%, mean 27%	20–23	Absent	Present	Absent	Unknown
<i>O. aequimanus</i>		Uniformly broad, spans ventral ~30% eye circumference	21–31%, mean 28%	19–23	May be present from ML 90 mm	Absent	Reduced	Absent from small patch (distal ~15% ML)
<i>O. compacta</i>		Broad posteriorly, narrow and rounded anteriorly	20–23%, mean 21%	20–23	Present (by ML 60 mm)	Absent	Absent*	Absent from large patch (distal ~40% ML)
<i>O. borealijaponica</i>		Uniformly broad, spans ventral ~30% eye circumference	24–31%, mean 27%	23–28	Present (small)	Absent	Absent	Present
<i>O. meridiopacifica</i>		Uniformly broad, spans ventral ~25% eye circumference	16–22%, mean 19%	15–19	Absent	Present	Present	Present
<i>O. lacrima</i> sp. nov.		Broad posteriorly, tapered to point anteriorly	26–32%, mean 29%	20–24	Present (by ML 50 mm)	Absent	Absent	Present
<i>O. prolata</i> sp. nov.		Uniformly broad, spans ventral ~50% eye circumference	28–40%, mean 36%	20–23	Absent	Present	Present	Present

\* consistent in majority of material examined, although anomalous reduced band was present in several specimens from north Hawaiian waters; \*\* chromatophores faded and/or indistinct in all material examined



## DISCUSSION

The systematic confusion historically associated with the genus *Onychoteuthis* is partially resolved by these findings, although additional taxa may inhabit the regions more poorly represented in the material available, especially the eastern tropical and southeastern Pacific. Each character state previously used to separate "*O. banksii*" from congeners [e.g., large, circular visceral photophores, 20–23 tentacular hooks, a slender muscular mantle with fins extending over 55%–60% ML, arms 35%–45% ML; see Nesis (1987) and Kubodera et al. (1998)] is shared by various groupings of three to four of the presently reported Pacific taxa. No single character or character state is diagnostic on its own, but the combined patterns of chromatophore distribution, tentacle morphology, and photophore morphology (summarized in Table 8) allow identification of these otherwise similar Pacific congeners, and may assist in unraveling more of the *O. banksii* complex in the future.

Young and Harman (1987) first reported chromatophore patterns to be species-specific in the genus *Onychoteuthis*, using them to differentiate three species of Hawaiian paralarvae. Certain (different) chromatophore patterns now also appear species-specific in subadults of these and other *Onychoteuthis* species. In the 200 specimens examined for this study, the presence/absence of chromatophores along the oro-ventral tentacle stalk ridge, and in a wedge across the oral face of the tentacle stalk, proximal to the carpus (see Fig. 59), are quite consistent within species; however, several specimens of *O. compacta* from North Hawaiian waters possess a small number of chromatophores proximal to the carpus, where other *O. compacta* specimens do not. The presence/absence, and size, of an unpigmented distal patch on the ventral mantle surface are also consistent within species, and may prove useful in rapid differentiation of taxa, in specimens where the chromatophores are in good condition. However, since undamaged specimens are rare, and chromatophores may fade substantially even in initially undamaged material, these patterns should be considered in concert with other more durable characters.

In addition to chromatophore patterns, reliable differences between taxa are observed in club length (compared to ML), overall number of hooks on the club, presence/absence of a ventral basal spike in the distal-most ventral hooks, and overall hook shape, including length (relative to club length) and shape in lateral profile. Although many of these character states are shared between two or more taxa, several species possess at least one unique character state (e.g., low number of hooks, 15–19, in *O. meridiopacifica*; high number of hooks, 23–27, in *O. borealijaponica*; and consistently shorter clubs, 20%–23% ML, in *O. compacta*).

*Onychoteuthis* is the only onychoteuthid genus reported to bear photophores. The shape of the visceral photophores has been used previously to differentiate *O. borealijaponica* from other *Onychoteuthis* species; *O. meridiopacifica* also has "very small," oval-shaped visceral photophores (Kubodera et al., 1998; Vecchione et al., 2003, herein). *Onychoteuthis lacrima* sp. nov. was first recognized as distinct from the other species treated herein based on the tear-drop-shaped posterior photophore, while the similar-sized anterior and posterior photophores in *O. aequimanus* and *O. prolata* sp. nov. facilitate their differentiation from *O. compacta*. Furthermore, examination of ocular photophores reveals slight differences in morphology, including the extent of eye circumference covered by the photophore, and the shape and breadth of the anterior end compared to the posterior end. It may be that the pres-

ence and diverse shapes of the visceral and ocular photophores, all visible through the ventral tissues of the body in life (Vecchione et al., 2003), aid in recognition and positioning of conspecific individuals during mating, since *Onychoteuthis* is the only onychoteuthid genus known to embed spermatophores in consistently located longitudinal ventral cuts on the mantle [pers. obs., Okutani and Murata (1983), Okutani and Ida (1986)].

Roeleveld (South African Museum, unpubl.) observed that the ocular photophore in some paralarval and juvenile (South African) "*O. banksii*" specimens first appears as two separate patches, which later unite into the bar- or crescent-shaped organ typical of *Onychoteuthis* species. Young and Harman (1987) also report this condition for *O. spp.* "B" and "C," yet for *O. compacta* a single ocular photophore is present from at least ML 8.9 mm. Thus it appears that early development patterns of the ocular photophore may be species specific, which may help identify these *Onychoteuthis* species in early ontogenetic stages.

In addition to describing the buccal morphology of the two new species, the lower beaks, radulae, and palatine palps of four previously recognized species are also described. The beaks of all *Onychoteuthis* species examined thus far are robust, with relatively short LRLs (compared to overall beak size; LRL < 60% wing length in all species), and have prominent anterior lateral wall ridges. Some variation was observed within species; the lower beaks of larger *O. compacta* (ML > 75 mm) may take the "normal" form in the crest and hood region (Figs. 25A–C), or the crest may be produced ventrally into a large, rounded "hump" that appears to stretch the posterior margin of the hood (Figs. 25D,E). Candela (unpubl. data) observed similar variation in lower beaks of Atlantic *O. "banksii"* (not sensu stricto, pers. obs.) and ascribed it to sexual dimorphism, believing it to occur solely in female beaks. It has since been observed in males as well (pers. obs.), though to a lesser extent, suggesting that sexual dimorphism in the beaks may occur, as it has been reported in other onychoteuthid genera (Bolstad, 2006). The relatively small number of beaks examined in this study (e.g., for *O. prolata* sp. nov., N = 13) may simply not have included specimens displaying pronounced sexually dimorphic characters or character states.

Regarding the remaining buccal characters, apparent correlations were observed between radular and palatine tooth morphology. The six *Onychoteuthis* species fall into two groups: those with clearly tricuspid rachidian teeth, with pronounced lateral cusps (*O. aequimanus*, *O. compacta*, *O. meridiopacifica*, Figs. 19, 26, 43), all possessing a low number of palatine teeth (~25–45); and those with unicuspid or only slightly tricuspid rachidian teeth, with low, indistinct lateral cusps (*O. banksii*, *O. borealijaponica*, *O. lacrima*, Figs. 10, 34, 52), each possessing 65–70 palatine teeth. As the distributions of these two groups are oddly disjunct and little dietary information is available for these taxa, the significance of this correlation is unknown. However, Bonnaud et al. (1998) found that *O. compacta* and *O. lacrima* sp. nov. fell into separate groups.

In the other onychoteuthid genera for which radular and palatine morphology have been reported (Bolstad, 2007), the opposite correlation between rachidian morphology and number of palatine teeth is observed—*Moroteuthis ingens* (Smith, 1881) and *Moroteuthis robsoni* Adam, 1962, both with a tricuspid rachidian, possess a relatively high 60–65 palatine teeth, while *Notonykia africanae* Nesis, Roeleveld, and Nikitina, 1998 and *Notonykia nesisi* Bolstad, 2007, both with a unicuspid rachidian, with very similar radular morphology to the unicuspid *Onychoteuthis* species, pos-

sess ~45 palatine teeth. As palatine tooth morphology is reported and compared for the remaining onychoteuthid species, patterns in these apparent correlations and contradictions may emerge; however, it is presently unclear whether these character states indicate intrafamilial relationships, or diet peculiarities.

Several additional traditionally important characters were examined for this study, including gladius morphology and occipital folds. Although the gladii of several species are distinctive (particularly *O. meridiopacifica*, Fig. 45, but also *O. borealijaponica*, Fig. 36), those of the remaining five species are all quite similar (Figs. 12, 27, 54, 63), save minor differences in cross-section that are unlikely to be useful in distinguishing between these taxa. Gladius morphology therefore seems most relevant at the generic level, with the *Onychoteuthis* gladius characterized by being narrow (width < 10% GL), with a relatively long free rachis (18%–40% GL), deep, solid dorsal keel distally, and a short rostrum (< 5% GL), narrow in dorsal profile, triangular in lateral profile.

Similarly, while the high number of secondary occipital folds (generally seven to nine) is unique to *Onychoteuthis* among onychoteuthid genera, with only *Ancistroteuthis* and *Notonykia* otherwise reported to bear secondary folds (and then a lower number, six or seven and three, respectively), few consistent variations in number or morphology were observed between species. Secondary occipital folds therefore also appear most useful in intergeneric, rather than intrageneric, comparisons.

The recognition of two new species in the *Onychoteuthis banksii* complex from limited samples (~380 specimens from 15 repositories) and geographic regions of the Pacific suggests that other regions and oceans from which "*O. banksii*" has been reported may also host distinct species. Preliminary examinations of central Atlantic material suggest the presence of at least three species, including *O. banksii* (sensu stricto), one species with long tentacle clubs similar to *O. prolata* sp. nov., and a third similar to *O. compacta*. Additional collecting of these problematic animals from all oceans would assist in resolving further systematic problems, and would contribute to greater understanding of the bathymetric and geographic distribution of all taxa.

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